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Fish and Wildlife Research 2

Spread, Impact, and Control of Purple Loosestrife (*Lythrum salicaria*) in North American Wetlands

UNITED STATES DEPARTMENT OF THE INTERIOR
FISH AND WILDLIFE SERVICE

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Fish and Wildlife Research

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Front cover: *Upper photo.* Pump house and water control structure for green-tree impoundment at Montezuma National Wildlife Refuge in central New York. Waterfowl broods produced in adjacent flooded forest found excellent foraging conditions among floating and emergent aquatic plants in foreground, 18 June 1968. *Lower photo.* Ten years later, purple loosestrife had displaced native food and cover plants in the waterway surrounding the green-tree impoundment at the Montezuma Refuge. Biologist holding stadia rod in middle foreground is obscured by mature plants. Note the abundance of *Lythrum salicaria* seedlings along the water line, 16 August 1978.

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Spread, Impact, and Control of Purple Loosestrife (*Lythrum salicaria*) in North American Wetlands

By Daniel Q. Thompson
Ronald L. Stuckey
Edith B. Thompson

UNITED STATES DEPARTMENT OF THE INTERIOR
FISH AND WILDLIFE SERVICE
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Foreword

After more than 50 years of study and debate, purple loosestrife (*Lythrum salicaria*), an emergent aquatic plant, has come to the forefront in marsh management discussions in the eastern and midwestern United States. The relatively recent and rapid westward expansion of the plant and its rise to dominance in many inland marsh and river systems are causes for alarm among botanists, wetland ecologists, and waterfowl managers. With nearly 190,000 hectares of wetlands being lost annually in the conterminous United States, it is imperative that the remaining habitat realize its optimum productivity. Unfortunately, purple loosestrife's strong competition with and replacement of other, more desirable aquatic emergents has led to a decline in wildlife food and cover values in many wetlands.

This report documents the spread and impacts of purple loosestrife in North America. It details the authors' research and personal observations and synthesizes a vast body of literature on *L. salicaria*. The publication should serve many purposes. First and foremost, it will be a valuable source book for all biologists interested in loosestrife ecology. It should also encourage additional research to find acceptable and effective ways of controlling purple loosestrife. Finally, the report will be of practical use to wetland managers facing the threat of loosestrife invasion.

In addition to being a comprehensive treatise on the accumulated body of knowledge on purple loosestrife, this publication serves to illustrate two fascinating phenomena. The first is the degree to which certain species can adapt to and colonize new environments. *L. salicaria* owes much of its rapid spread across North America to its wide tolerance of varying physical and chemical conditions, such as those characterizing disturbed habitats. The species also is a prolific seed producer and uses many mechanisms for seed dispersal. Second, the story told herein emphasizes how much we can impact our environment. *L. salicaria* seeds originally reached North America in the cargo and ballast of ships coming from Europe. Rootstalks may also have been brought in by horticulturists. The plant subsequently spread to interior wetlands by way of canals, irrigation ditches, and roads. Its use in horticulture and beekeeping industries has also expanded the range of the species. Thus, human activities, combined with loosestrife's physiological and ecological adaptability have led to its present day distribution in North America.

As a wildlife resource professional, I am concerned about the growing evidence that waterfowl, furbearers, and other wetland-dependent species are being adversely impacted by loosestrife. The resulting biological, recreational, and economic repercussions are disturbing; however, the authors offer hope. They review methods that can be applied locally by wetland managers to minimize the expansion of *L. salicaria* and to cope with existing infestations. Some States have designated the plant a noxious weed. Convincing arguments are also made for the development and implementation of a biological control program to address the loosestrife invasion. The favorable cost–benefit ratio presented provides food for thought. Clearly, a long-term solution is needed if this major ecological problem is to be halted. The suggested increased emphasis on research on biological control methods should receive immediate attention by concerned natural resource agencies.

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Spread, Impact, and Control of Purple Loosestrife (*Lythrum salicaria*) in North American Wetlands

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Abstract

Purple loosestrife (*Lythrum salicaria* L.) is an emergent aquatic plant of Eurasian origin; with the rise of marine commerce, it became established on all mid-latitude continents, except South America. *L. salicaria* arrived along the northeastern maritime coast early in the 19th century and has subsequently spread across mid-latitude North American wetlands. Several modes of colonization or escape were probable, including ship's ballast, livestock bedding and forage, wool, and purposeful import as seeds or rootstocks for early gardens and herb beds. The gene pool shared by these immigrants accumulated over 50 years or more from a wide climatic and geographic range across Europe and Asia Minor. Rapid gene flow is inferred from the more or less equal distribution of three forms of flowers (short-, mid-, and long-style) occurring over Europe and North America. Purple loosestrife's plant associates in North America are cattails (*Typha* spp.), reed canarygrass (*Phalaris arundinacea*), sedges (*Carex* spp.), bulrushes (*Scirpus* spp.), willows (*Salix* spp.), and horsetail (*Equisetum fluviatile*), in the order mentioned. All of these plants have conspecifics (or nearly identical taxa) that are native to Eurasia, suggesting that *L. salicaria* was strongly preadapted to be a successful immigrant.

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The bisexual flowers of purple loosestrife are insect-pollinated. Self-pollination is possible, but cross-pollination prevails. The period of bloom in most areas is from late June to early September. An old plant can produce more than 2 million seeds per growing season; sexual reproduction is of overwhelming importance. Seed dispersal is largely by drift in moving water; long distance spread is possible by seeds imbedded in mud on water birds, trucks or off-road vehicles, or in the cooling systems of outboard motors. Erratic spread can also occur by purposeful introduction as a honey bee forage plant or by accidental escape from horticultural plantings. Seed samples from commercial suppliers of wildlife cover and prairie restoration plants have contained purple loosestrife seeds as an impurity. Seed longevity is at least 3 years with viability of 80 + %. Floating seeds or propagules must lodge on open, moist soil or saturated organic debris to take root. Once established, purple loosestrife can survive with 50% of full sun, but declines in vigor at lower light levels. The plants grow on a wide range of substrates, but are more successful on slightly acid or neutral soils. *L. salicaria* has many ways of adapting to a wide range of habitats. It responds to soil nutrient (P and N) deficiencies by increasing the root to shoot ratio, to rising water level by the growth of aerenchyma in submerged stem tissue, and to trampling, cutting, or crushing of stems with shoot and root buds at the site of damage.

The spread and dominance of purple loosestrife in North American wetlands has shown a pattern of exponential increase that corresponds to the rate of exploitation of these habitats. With the construction of the eastern canal systems, and the extension of marine commerce into the Great Lakes, *L. salicaria* colonized the glacial marshes of the Midwest by 1900. By 1940, it was established in the Pacific Northwest and had begun to spread onto the Great Plains; by 1985, Alaska and Montana were the only States north of the 35th parallel that had not reported purple loosestrife.

The impact of purple loosestrife on native vegetation has been disastrous, with more than 50% of the biomass of some wetland communities displaced. Monospecific blocks of this weed have maintained themselves for at least 20 years. Impacts on wildlife have not been well studied, but indicate serious reductions in waterfowl and aquatic furbearer productivity. Several declining species of vertebrates are threatened with further degradation of their breeding habitats with the continued expansion of purple loosestrife. The plant's low palatability to livestock makes it a problem in wetland pastures in the Northeast; it also threatens riparian hay meadows and off-water swales in irrigated areas in the West. Although *L. salicaria* can invade relatively undisturbed habitat, the spread and dominance of this weed have been greatly accelerated in disturbed habitats. Despite early control efforts in Quebec, and subsequent work in the United States, little research on purple loosestrife ecology and control has been done. Glyphosate has been used successfully, but no effort has been made to measure the impact of this broad-spectrum herbicide on native plant communities. Enough preliminary work has been done with biological control of purple loosestrife to suggest that this promises to be a valuable approach.

On both regional and local scales, the rate of spread of *L. salicaria* has followed the logistic curve. At present, coping with purple loosestrife hinges on early recognition of the arrival of the weed and a conservative pattern of marsh management that avoids stressing native plant communities. Early detection allows local eradication to be carried out with minimum damage to the native plant community. Some form of integrated control is needed. California, Illinois, Ohio, Minnesota, and Wisconsin have taken prompt action to deal with this weed.

Purple loosestrife (*Lythrum salicaria* L.) is an erect, herbaceous perennial of Eurasian origin that became established in the estuaries of northeastern North America by the early 1800's. By the late 1800's it had spread throughout the northeastern United States and southeastern Canada, reaching as far north and west as Manitoba. *L. salicaria* caused few problems until the 1930's when it became aggressive in the floodplain pastures of the St. Lawrence River. Since then, it has steadily expanded its local distribution and now poses a serious threat to native emergent vegetation in shallow-water marshes throughout the northeastern and north-central regions. Recent records indicate that purple loosestrife is also tolerant of soils and climates beyond these regions and threatens to become a serious problem in wetlands and irrigation systems in the Great Plains and the Far West.

It is no small irony that after 50 years of struggle to find some means of breaking up monotypic stands of cattails (*Typha* spp.) to increase wildlife diversity and abundance, wetland managers must now cope with a foreign species that replaces cattail, but unfortunately creates another monospecific community of greatly diminished wildlife value.

Field Identification, Classification, and Distribution

The name "loosestrife" has been associated with several members of the loosestrife family (Lythraceae) as well as with the genus *Lysimachia* in the primrose family (Primulaceae). Although *Lythrum salicaria* has more than 10 common names in America and Great Britain, the most widespread and best established usage is "purple loosestrife." *L. salicaria* (Fig. 1) is most easily identified during its long season of bloom (late June to early September in most areas). At this time, the characteristic reddish-purple floral masses can be easily identified at 100 m. In North America, purple loosestrife may be confused with one of the following: fireweed (*Epilobium angustifolium*), blue vervain (*Verbena hastata*), blazing stars (*Liatris* spp.), and in the Pacific Northwest, spirea (*Spiraea douglasii*). Nevertheless, once observers sharpen their search images for the subtle differences in color and floral structure between these plants, positive field identification is easy. Differences in site preferences also help to separate purple loosestrife from superficially similar species; *L. salicaria* usually occurs on moist or saturated soils. Moreover, it is the only reddish-purple flowered plant to develop massive monospecific blocks of showy floral displays over large wetland tracts. In early autumn, a distinctive but transitory color change usually occurs at the end of the growing season when *L. salicaria* leaves dehydrate and turn bright red; this color may persist for 10 days. Dead stalks remain standing through winter and have a characteristic brown tone that, in combination with spire-shaped capsule clusters, readily identifies the species.

Classification

Lythrum is the type genus of the loosestrife family (Lythraceae). About 22 genera and 500 species occur worldwide; representatives include herbs, shrubs, and trees that reach their greatest abundance in the American tropics where two of the largest genera (*Cuphea* and *Diplusodon*) are endemic (Gleason 1963). Several of the genera include species that are cultivated as ornamentals, but none are food or fiber producers. About 35 species of *Lythrum* occur throughout the world; Shinners (1953) recognized 12 species in his synopsis of *Lythrum* in the continental United States. He concurred with most American botanists that 3 of these 12 species (*L. hyssopifolia*, *L. virgatum*, and *L. salicaria*) were nonindigenous. *L. hyssopifolia*, an annual, very likely came from Europe where it is listed as a weed in seed of clover and lucerne (Salisbury 1961). We found no mention of *L. hyssopifolia* as an agricultural weed in North America, despite its widespread occurrence in waste places and disturbed wetlands.

L. virgatum is a purple-flowered loosestrife, somewhat similar to *L. salicaria*, but distinctive in that it is glabrous throughout, with leaves narrowed at the base. The leaves of *L. salicaria* are wide (cordate) at the base and more or less covered with fine hairs (downy). Fernald (1950) considered *L. virgatum* to have come from Europe, and to have escaped from cultivation in local areas in Massachusetts and New Hampshire; it does not seem to be spreading beyond these areas. Hultén (1971) suggested a close relationship between *L. virgatum* and the nearly glabrous races of *L. salicaria* recognized by Hara (1956) from the USSR and Japan. Shinners (1953) was not able to obtain North American specimens of *L. virgatum*, but, from examination of three Eurasian specimens he concluded that they were "not very similar to *L. salicaria*, many of the flowers being solitary or merely paired."

Hultén (1971) considered the several races of *L. salicaria* occurring over the world to be difficult to distinguish, especially on the basis of pubescence. He referred to the *L. salicaria* complex and noted that its variability was also reflected in reports of chromosome numbers of 30, 50, and 60. Although we did not attempt to evaluate the genetic status of the *L. salicaria* complex in North America, we examined specimens of *L. salicaria* from nearly all sectors of its continental range in North America and found that, morphologically, they were fairly uniform with all of the specimens assignable to *L. salicaria*. Moreover, the work of Shamsi and Whitehead (1974*b*) showed that *L. salicaria* responds to a decrease in light intensity with increased leaf area and decreased amount of tomentum. This suggests that some of the variability reported in herbarium specimens may have been influenced by light levels at the site of collection. We recognize that the variability of *L. salicaria* needs investigation, but believe that we are dealing with a well-defined species. From this perspective, we are thankful not to be struggling with the high degree of variability characteristic of the leafy spurge (*Euphorbia esula*) complex (Croizat 1945) wherein 11 closely related taxa have been identified in collections of this widespread and pernicious agricultural weed.

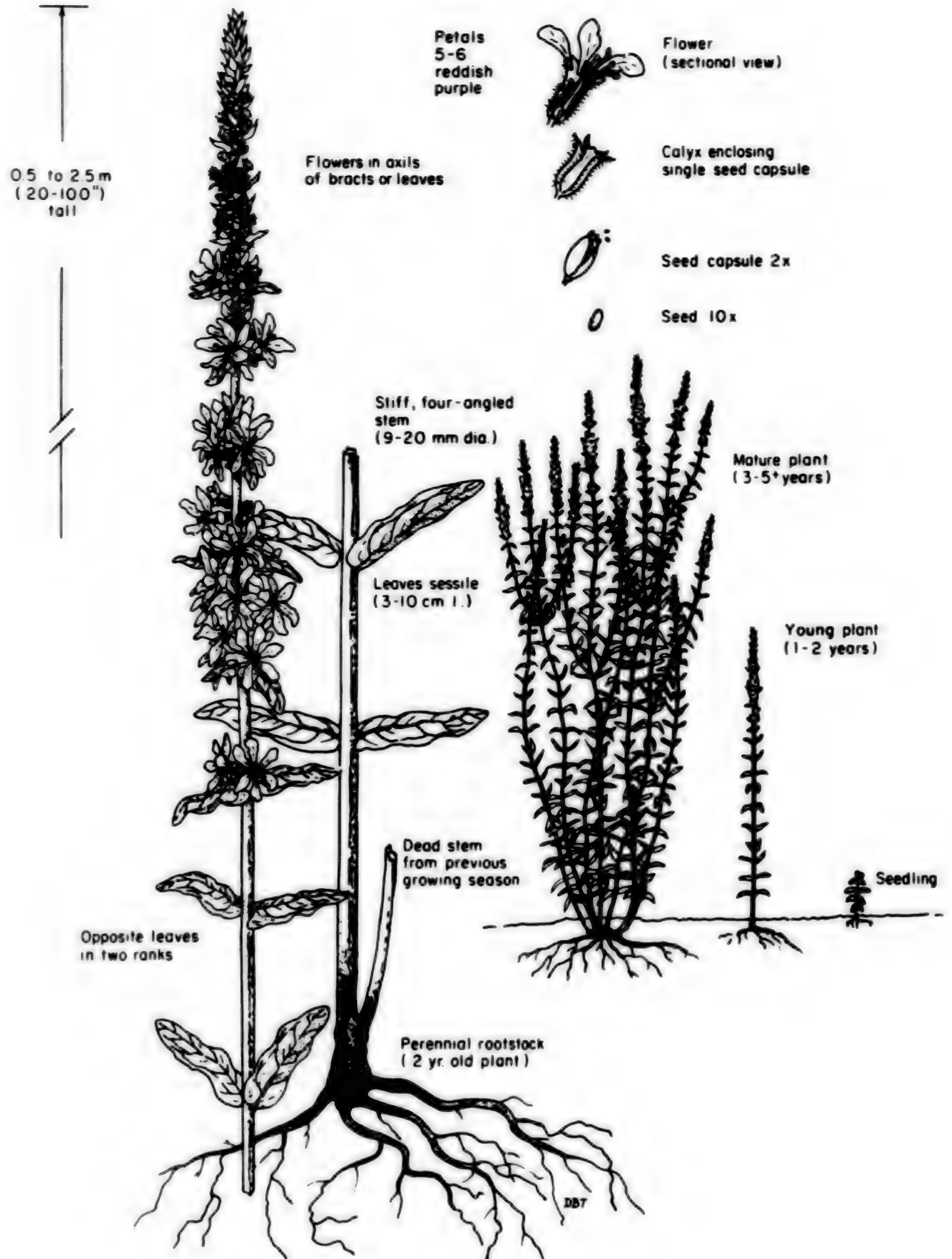

Fig. 1. Structure, growth forms, and field identification characters of *Lythrum salicaria* (purple loosestrife).

Origin and World Distribution

Although the geographical origins of *L. salicaria* are uncertain, Hultén (1971) showed European and Asian centers of distribution (Fig. 2). The European segment is much the larger and extends from Great Britain across Europe to the Central USSR. *L. salicaria* is abundant in England, Wales, and Ireland but becomes rare in Scotland (Clapham et al. 1962; Perring and Walters 1976). It reaches its northwestern limit of occurrence near Sogne Fjord on Norway's North Sea coast and extends through southern Sweden and Finland into Russia with its northern limit near the 65th parallel. It is common throughout central and southern Europe (Palhinha 1939; Polunin 1969), but is not known from the Azores, Balearic Islands, Crete, the Faeroes, Iceland, or Svalbard (Tutin et al. 1968). In the Mediterranean basin it occurs in northern Morocco and along the coastal fringe of Algeria. It is common, although not abundant, in Italy (D. Q. Thompson, 1984 unpublished field notes). It continues eastward through the Balkans to the western shore of the Caspian Sea. Zohary (1972) reported purple loosestrife to be "locally fairly common" in riverbank and swamp habitats in Palestine.

North and east of the Caspian Sea, a considerable gap in the distribution of *L. salicaria* occurs in arid western Mongolia, western and central China, and Tibet. Hultén (1971) indicated the main islands of Japan as the core of the Asian segment of the species' native range, with outlying populations extending from the Amur River south across the lowlands of Manchuria and China to Southeast Asia and northern India. In historic times, *L. salicaria* has expanded to a circumpolar distribution in the northern hemisphere, a pattern shown by Hultén (1958, 1971) to be typical of more than a hundred other European or Asian dicots. *L. salicaria* has also invaded other temperate and subtropical areas and is now known in eastern Africa (Ethiopia), Australia, and Tasmania. In an atlas of world weeds, Holm et al. (1979) showed *L. salicaria* as present in New Zealand. We are not aware of confirmed *L. salicaria* records in South America or South Africa. As with many weeds, the distribution and timing of the spread of *L. salicaria* suggest a close association with exploration and human emigration from northern Europe and the development of international maritime commerce.

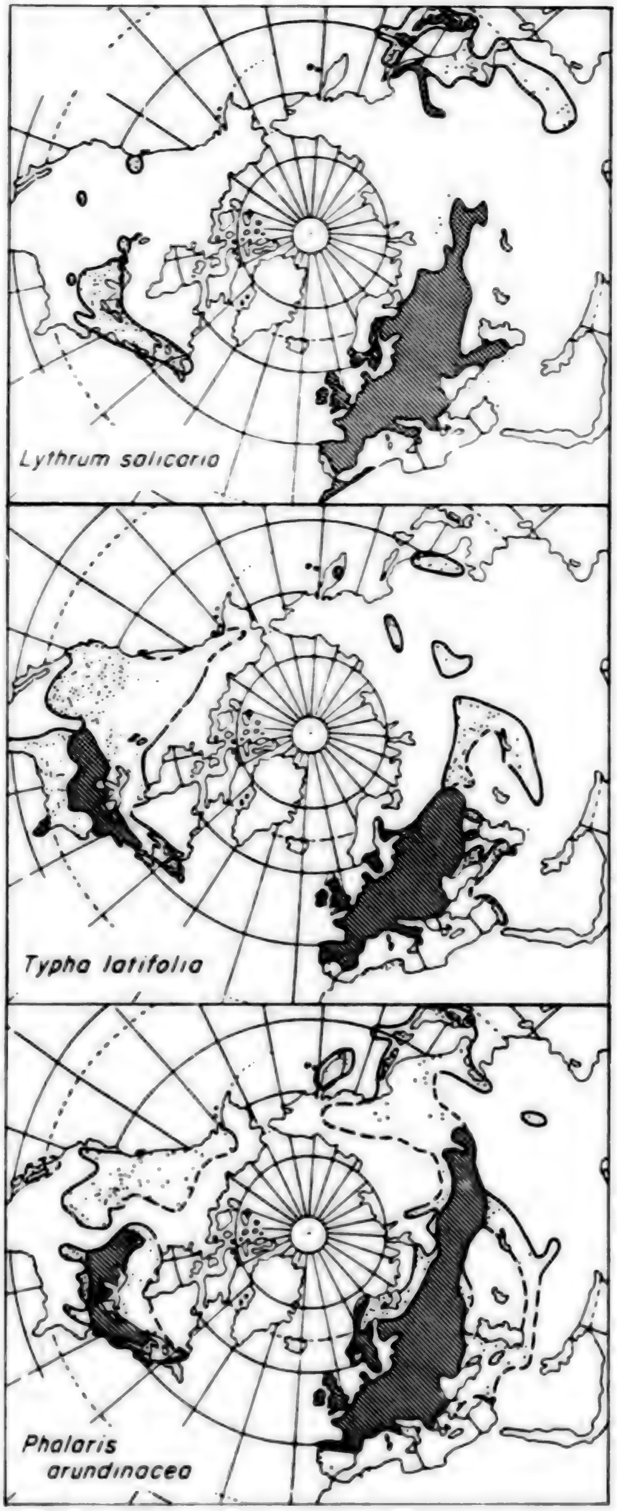

Fig. 2. Distribution of purple loosestrife (*Lythrum salicaria*), broad-leaved cattail (*Typha latifolia*), and reed canarygrass (*Phalaris arundinacea*), in the Northern Hemisphere (after Hultén 1964, 1971). Shaded areas indicate zones of more or less continuous distribution; dots represent collection sites; solid lines indicate probable outer distribution boundary; dashed lines are tentative outer limits.

Biology and Life History

A mature, long-established purple loosestrife plant is often 2 m high and 1.5 m wide. From 30 to 50 herbaceous stems rise from a common rootstock to make the graceful, wide-topped crown that is characteristic of these old-aged clumps. Although lateral growth of the root crown offers new sites of origin for peripheral stems, a natural limitation of about 0.5 m seems to be the maximum diameter obtainable by the root crown. Some confusion exists in the literature as to whether *L. salicaria* rootstocks can send out rhizomes. Ohwi (1965) described *L. salicaria* in Japan as "rhizomatous"; however, this may refer to adventitious buds arising on lateral roots. Describing marsh vegetation in England, Pearsall (1918) included *L. salicaria* as one of three shoreline species that "have tough rhizomes capable of penetrating the interstices of the hard substratum." Morse and Palmer (1925) did not mention rhizomes, but referred to rootstalks as "creeping extensively." We have seen lodged stems that have become buried under 10 cm of silt and sand following an unusually heavy June rainstorm. By late July, new shoots were appearing from adventitious buds on the buried stems, giving a convincing appearance of spread by rhizomes (Fig. 3). We have excavated purple loosestrife root crowns in many parts of its range in the United States and Canada, but have found no evidence of spread by rhizomes.

Bodmer's (1928) thorough work on the developmental anatomy of *L. salicaria* contained the suggestion that growth of some stem tissue can survive above the root-crown level for 2 or 3 years. We are unable to interpret these findings and can only comment that most standard botanical works describe *L. salicaria* as having perennial rootstocks and stout, erect, annual stems. There is evidence that surviving *L. salicaria* rootstalks occasionally fail to send up stems. Gilbert and Lee (1980) made annual counts of two populations and reported that in 14 instances "a plant was seen in one year, did not grow above ground in the next, but was present again...in the following year."

Flowering and Pollination

The trimorphic structure of purple loosestrife flowers attracted the attention of 19th-century naturalists. Darwin (1893) was intrigued by the plant and made some

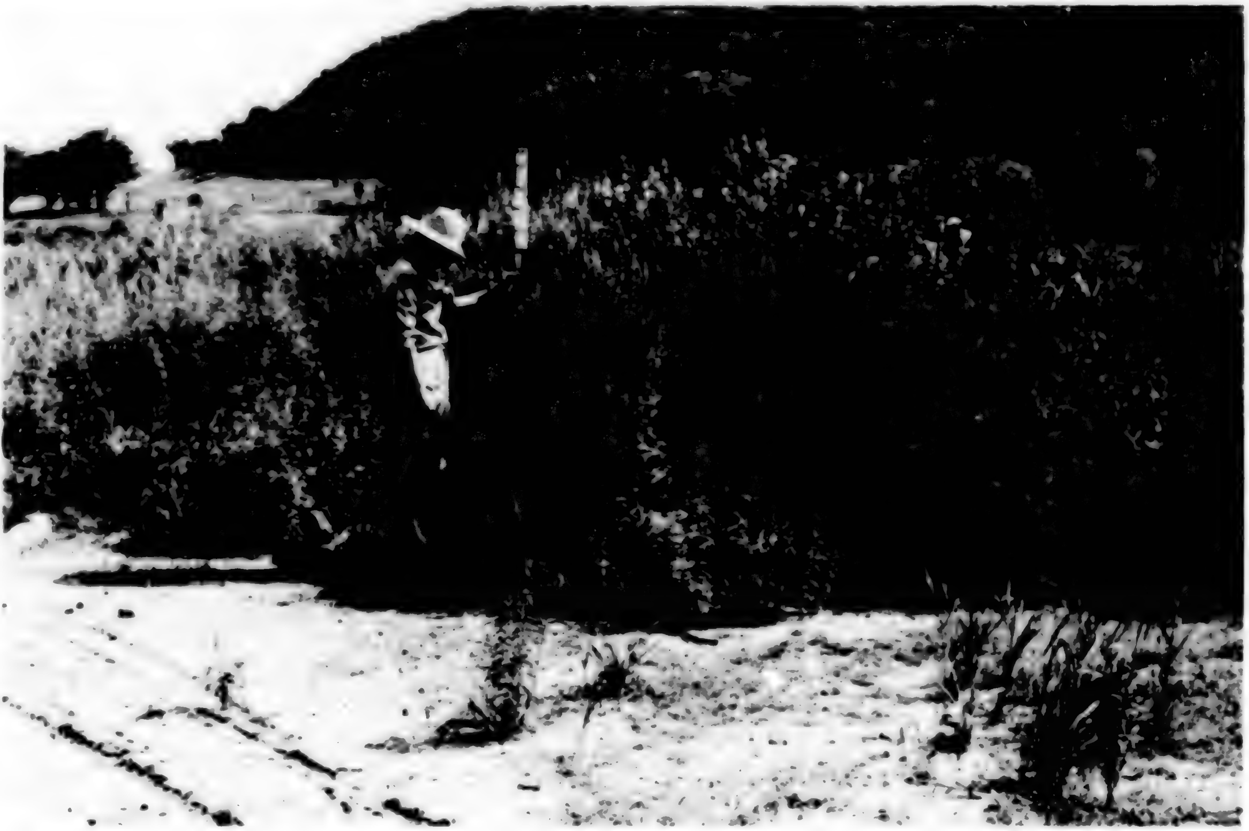

Fig. 3. Stems buried by a flash flood gave rise to adventitious shoots of *Lythrum salicaria* (*left foreground*) in this riparian pasture near Red Wing, Minnesota, 8 August 1978.

remarkably perceptive experiments and observations. He noted that three kinds of flowers occurred on *L. salicaria* plants and that three lengths of styles occurred with three combinations of anther lengths. He also noted that the three forms of flowers coexisted in wild populations in nearly equal frequencies. Many workers (East 1927, 1932; Haldane 1936; Levin and Kerster 1973) have since reported on inheritance and population genetics in *Lythrum*, but from the standpoint of weed ecology, one of the most significant contributions was by Halkka and Halkka (1974). They investigated the frequencies of the three style morphs in *L. salicaria* on small, isolated island populations in the Gulf of Finland. Despite the small size (0.1 km^2) and recent age of some of the habitats (± 100 years) all 16 populations studied contained the three style morphs in roughly 1:1:1 frequencies. They compared their findings with a summary of style morph frequencies from Great Britain, Germany, Switzerland, and the United States assembled by Schoch-Bodmer (1936) and concluded that the nearly identical results over a vast geographic area indicated that the vitality of the various genotypes did not depend on ecological conditions. Moreover, the highly similar frequencies indicated that sexual reproduction was of overwhelming importance in these populations. Although not sure how much of this gene flow could be attributed to pollen dispersal, Halkka and Halkka (1974) stated that seed dispersal seemed adequate "to keep *total* gene flow efficient." They also noted that their findings were in contrast with the report by Kuusvouri (M.S. thesis, University of Helsinki, Finland, 1960) of dense stands of *L. salicaria* wherein vegetative reproduction was common. These stands were on relatively fertile shore meadows and were characterized by a high frequency of mid-style morphs. The work of Shamsi and Whitehead (1974*a*) in Great Britain and our own observations in North America supported the findings of Halkka and Halkka (1974), that is, with the exception of locally disturbed areas (that may account for Kuusvouri's findings), sexual reproduction is of overriding importance in the establishment and spread of *L. salicaria*. Similarly, if asexual reproduction is of more than local importance, it occurs equally in all stylar morphs.

Heuch (1980) set up a simulation model to test the effect of restricted population size on the rate of random loss of various style morphs in *L. salicaria*. He concluded that isolated populations of 20 or more individuals would generally be quite stable and postulated that variations in the frequencies of the three forms may be caused by the unequal disappearance of one or more of the forms because of random effects.

Seed Production and Dispersal

The seed output of a purple loosestrife plant is dependent on its age, size, and vigor. Shamsi and Whitehead (1974*a*) gave the average number of seed capsules for their experimental plants as 900, with a yield of about 120 seeds per capsule. These data probably refer to first-year plants with single stems. Our observations on three mature (4–5 years old) transplants (from Nebraska and Wisconsin wetlands) at Fort Collins, Colorado, showed the mean number of stems to be 30, with 1,000 capsules per stem, and 90 seeds per capsule; the mean number of seeds produced per plant was estimated at 2,700,000. Capsules from early flowers produced ripe seed while the plants were still green. The flat, thin-walled seeds had no endosperm and were about 400 × 200 microns (Fig. 1).

Ridley (1930) noted that *L. salicaria* seeds sink upon being thrown into water, but rise to the surface following germination. He considered seed dispersal to be largely by means of floating seedlings. We agree with his conclusion on mode of dispersal, but find that not all seeds sink upon falling on water; some dispersal could be by floating, ungerminated seeds. Although Ridley did not include *L. salicaria* among plants whose seeds were dispersed by wind, Shamsi and Whitehead (1974*a*) declared that *L. salicaria* has wind-dispersed seeds. Nilsson and Nilsson (1978) used Sernander's (1901) work to classify *L. salicaria* as a species that was dispersed by wind over snow and ice. Surely the seeds are light enough (0.5–0.6 mg) to be carried by a strong wind, but we have observed that the densities of seedlings fall off sharply within the first 10 m from the parent plant, suggesting a very limited role for wind dispersal. Moreover, distribution from parent plant is most often downslope rather than downwind. The low mass and small size of *L. salicaria* seeds make them likely to be spread in mud adhering to aquatic wildlife, livestock, treads of all-terrain vehicles, boots of hunters, or on the hulls of skiffs or barges. They could also survive ingestion by waterfowl and other marsh birds or be carried in the cooling systems of outboard motors. Nevertheless, with the exception of Kerner (1902), there is no evidence to support any of these possibilities. Kerner's studies in Europe included *L. salicaria* in a list of 21 plants whose seeds he found in mud "obtained from the beaks, feet and feathers of swallows, snipe, wagtails, and jackdaws. . . ."

Correll and Correll (1975) mentioned ducks eating the seeds of *Decodon* and *Lythrum*. Torrey (1931) suggested that the relatively rapid, upslope spread of *L. salicaria* into small riverine wetlands was caused by blackbirds

(Icteridae) that had eaten the seeds of plants in the Hudson River lowlands. Last, the senior author has observed the spread of *Lemna* spp. into adjoining impoundments along the foraging trails of muskrats (*Ondatra zibethica*). In a similar way, seeds or propagules of *L. salicaria* could be spread by muskrats, waterfowl, or snapping turtles (*Chelydra serpentina*), as they move over dikes into adjoining impoundments.

Seed Longevity and Viability

Knowledge of the longevity and viability of purple loosestrife seeds and propagules under field conditions would be very useful to land managers attempting to cope with an infestation. As a test of their experimental procedures, Shamsi and Whitehead (1974*a*) measured the viability of the seeds used in their work. They compared seeds stored 3 years in dry condition in a refrigerator at 3–4 °C with freshly collected seeds. The stored seed began germination 2 days after fresh seed and reached maximum emergence (80 + %) on or about day 13. Fresh seeds reached maximum emergence (90 + %) on or about day 17. None of these differences was statistically significant. To our knowledge, no work exists on the survival and longevity of propagules. The low reserve of stored energy in *L. salicaria* seeds suggests that drifting germinated seeds would not survive beyond a few weeks; however, this matter needs study.

Germination

Shamsi and Whitehead (1974*a*) reported the critical temperature for germination of *L. salicaria* seeds to lie somewhere between 15 and 20 °C, with no germination occurring below 14 °C. They tested germination in short (9-h light, 15-h dark) versus long (16-h light, 8-h dark) day lengths and found no significant differences in percentage or speed of germination. Mitchell (1926) tested the effect of two light levels (diffuse and dark) in germination trials (at 20–25 °C) that used natural light and dark intervals for the diffuse treatment. In successive years, she found germination percentages of 84 and 67 in seeds in diffuse light versus 4 and 9 for seeds in dark. *L. salicaria* can germinate successfully on substrates with a wide range of pH. Shamsi and Whitehead (1974*a*) indicated germination down to pH 4.0. We observed successful development of young plants (germination implied) at pH 9.1 on the calcareous slope of an infested wetland near Powell, Wyoming.

Seedling Establishment

Floating seeds or propagules must fall or lodge against moist soil to begin a successful establishment. Bodmer (1928) reported that a 3-day-old seedling was about 3 mm long from the tip of the cotyledon to the extremity of the root. By 10 days, the seedling was about 6 mm long, with most of the growth in the primary root. By 20 days, the seedling was about 40 mm; the first true leaves appeared, and lateral and secondary roots had developed. By 25 days, stem elongation began with a 1–2-mm growth of the epicotyl; true leaves and vascular tissue were well developed. At this time, although the aboveground portion of the plant is less than 10 mm high, the young seedling could be well established. Directional growth is clearly indicated in Bodmer's sketches. We have observed this tendency in the elongating root crowns of first-year seedlings and noted that it was still apparent in 2- and 3-year-old plants. This directional growth may be the basis for the puzzling references mentioned earlier to the "rhizomatous" character of *L. salicaria*.

Most seedling establishment occurs in late spring and early summer when temperatures are high (Shamsi and Whitehead 1974*a*). These seedlings germinate from seeds or propagules that have survived at least one winter. Shamsi and Whitehead (1974*a*) found that summer-germinated seedlings in southern Great Britain did not produce more than four or five pairs of leaves and did not survive the following winter.

Growth Requirements

Shamsi and Whitehead (1974*a*, 1974*b*, 1977*a*, 1977*b*) carried out a series of laboratory and field experiments in their investigation of the factors determining the ecological and geographical distributions of *Epilobium hirsutum* (great hairy willow-herb) and *L. salicaria*. Both of these erect, perennial herbs are pioneers in marsh and fen communities in the British Isles. Optimum substrates for the growth of *L. salicaria* are moist soils of neutral to slightly acid pH. Nevertheless, we have found the plant growing in such a wide range of soil textures and types as to suggest that moisture is the most important factor for growth and reproduction. Parent materials invaded by purple loosestrife in North America varied from rock crevasses to gravel, sand, clay, and organic soils. Some of the least vigorous plants (50 cm tall) were growing on crushed-rock ballast on a railroad bridge near Lowell, Massachusetts. Some of the tallest specimens

(300 cm) were growing on alluvial sand near Elm Creek, Nebraska; these are among the largest plants that we have encountered in the North American range.

Light Intensity and Photoperiod

Our field observations indicated that purple loosestrife can survive in 50% of full sun, but declines in vigor and fails to reproduce at lower light levels. Shamsi and Whitehead (1974*b*) reported that both light intensity and photoperiod had marked effects on the growth of *L. salicaria*. Under three levels of light (100, 70, and 40%) over a 16-h day, they observed decreased fruit and seed production with each reduction in illumination. *L. salicaria*'s response to reduced illumination was a progressive increase in leaf size and a decrease in amount of tomentum and leaf thickness. These authors also noted that *L. salicaria* responded to reduced light by increasing the dry weight production of chlorophyll per unit leaf area. This compensation was seemingly enough to sustain total dry-weight production through roughly half of the experimental harvests. Reduction to 70% of full light caused very little change in growth or function; however, at 40% there was a significant reduction in mean dry weight of seed produced.

Shamsi and Whitehead (1974*b*) reported very different responses between *Epilobium hirsutum* and *L. salicaria* to a range of photoperiods of 9–16 h. *E. hirsutum* responded to all increments of reduced day length with extensions in growth. Its critical day length for flowering was 14 h. *L. salicaria* showed no growth responses in 10-, 11-, and 12-h photoperiods, but made an abrupt elongation of its shoots in the 13-h treatment when the critical point for flowering was reached.

Nutrients

The wide range of soils colonized by *L. salicaria* in North America is reflected in Shamsi and Whitehead's (1977*a*) experiments with comparative mineral nutrition of *L. salicaria* and *E. hirsutum*. *L. salicaria*'s growth in a standard nutrient solution was much less reduced with successive dilutions than *E. hirsutum*'s. The former responded to each level of dilution with an increase in root to top ratio. These authors also ran a similar experiment that tested *L. salicaria* and *E. hirsutum* responses to deficiencies in phosphorus (P), nitrogen (N), and potassium (K). As in their previous experiment, standard nutrient solutions were used, but the amounts of P, N, and K were reduced while all other nutrients were held at normal level. With successive dilutions, the growth of *L. salicaria* was more reduced by N deficiency than by P or K deficiencies, whereas *E. hirsutum* was sensitive to reductions of each of these elements. *L. salicaria* responded (as did *E. hirsutum*) to reductions in P and N, with an increased root to shoot ratio. In flower and fruit production, *E. hirsutum* was sensitive to reduction in all elements, whereas *L. salicaria* produced flowers at all levels of P deficiencies.

Temperature and Interspecific Competition

Shamsi and Whitehead (1977*b*) also studied the effects of temperature and interspecific competition on the growth of *L. salicaria* and *E. hirsutum*. They found that although both species produced similar dry weights and leaf areas under controlled growth conditions at 18°C, *L. salicaria*'s growth was far more restricted by low temperatures (8°C). In greenhouse experiments at 25°C, they reported that *L. salicaria* was a more successful competitor than *E. hirsutum* in standard and diluted nutrient solutions. Similarly, under field conditions, *L. salicaria* seedlings planted in early summer in soils of low fertility were superior competitors against *E. hirsutum*. However, in a field experiment on fertile fen soil that included the low temperatures of both autumn and spring, *E. hirsutum* was the more successful species in the following growing season.

In summary, Shamsi and Whitehead (1977*b*) observed that "Given higher temperatures, *Lythrum salicaria* survives and grows faster than *Epilobium hirsutum* on nutrient-deficient media and soils." They also noted that the confinement of *E. hirsutum* to base-rich fens and its complete exclusion from less fertile sites (in British Isles) can be related to its high nutrient demands. Although these authors did not attempt to compare the ecological distribution of *E. hirsutum* and *L. salicaria* in North America, their conclusions on mineral nutrition may in part explain the strikingly different behavior of these two aliens on this continent. Both species arrived from Europe more than 150 years ago and became naturalized in the Northeast. Subsequently, *L. salicaria* spread across the continent and is now established in all of our major river basins except the Arkansas, Colorado, and Rio Grande. Meanwhile, *E. hirsutum* continues to occupy a somewhat limited range in the Northeast and has gradually spread westward (Stuckey 1970); northern Illinois was its farthest westward spread into the Great Lakes region by the late 1960's. Stuckey considered the appearance of *E. hirsutum* in the State of Washington in the late 1960's to be the result of accidental rather than natural spread. Temperature may be a limiting factor in the northern distribution of *L. salicaria* in North America. Within the average annual minimum temperature map displayed by Bailey and Bailey (1976), *L. salicaria* has been a vigorous colonizer as far north as the − 29 to − 23°C zone; it has been less vigorous in the − 34.5 to − 29°C zone.

Shamsi and Whitehead (1974*a*, 1974*b*, 1977*a*, and 1977*b*) did not include soil moisture in their comparative eco-physiology studies of *E. hirsutum* and *L. salicaria*. Although soil moisture may not affect the wide geographic limits of these species, it can be an important factor in the position of each plant in local habitats. The senior author (D. Q. Thompson, 1984 unpublished field notes) observed that in central Italy and eastern Austria, *L. salicaria* grew on the hydric side of a soil moisture gradient. On the gently sloping shores of Lake Trasimeno (Italy) this difference was enough to place the species in separate but adjoining vegetation zones along the north side of the lake. Similarly, in a fallow field 0.5 km west of Trevi (Italy) numerous *E. hirsutum* and *L. salicaria* were growing together along the edge of a narrow ditch; however, great hairy willow-herbs were rooted in the topsoil on the edge of the ditch, whereas purple loosestrifes were rooted at the mean waterline in the ditch, about 30 cm below the position of *E. hirsutum*.

Ecology of Spread and Dominance

Habitats and Plant Associates

Shamsi and Whitehead (1974*a*) described the usual habitats of *L. salicaria* in Europe as "confined to wet, marshy places, coastal areas, stream banks and ditches." In England, Pearsall (1918) reported purple loosestrife to be frequent in reed-swamps and abundant in mixed fens where its associates were *Typha latifolia*, *Phalaris arundinacea*, and *Carex elata*, among others. Pearsall also listed *L. salicaria* as locally abundant in open carr where *Alnus glutinosa* and *Salix cinerea* were subdominant, decreasing to "frequent" in closed carr where *S. cinerea* became dominant. Purple loosestrife was also reported "along the margins of bogs near *Sphagnum*, *Erica*, *Tetralix*, *Narthecium ossifragum* and other calcifuge species" (Shamsi and Whitehead 1974*a*).

L. salicaria's affinity for wetland habitats in Europe is closely reflected in its invasion of North American sites. Freshwater marshes, open stream margins, and alluvial floodplains are its optimum habitats in the northeastern and north-central United States and adjacent Provinces in Canada. Most of the associates of *L. salicaria* in Europe and Asia are also abundant in temperate North America. Not surprisingly, they are also its most important associates in North American wetlands. Table 1 was constructed from photo and field notes of the senior author describing 45 sites across North America. All species occurring within a 1-m radius of the *L. salicaria* plant were listed as associates. Although the data represent inland habitats more than coastal wetlands, a pattern of association is apparent. *Typha* spp. were the most common associates, but declined somewhat in importance from east to west. Overall, *T. latifolia* occurred at 47% of the collection sites. Narrow-leaved cattail (*T. angustifolia*) occurred at only 4 of the 45 sites (9%). Reed canarygrass was overall the second most important associate. It increased in importance from east to west and became the most typical associate of *L. salicaria* in the Pacific Northwest. Sedges and rushes were the next most common associates in all three regions; *Salix* spp., *Phragmites australis, and Equisetum fluviatile* were present at about 9% of all sites.

Adaptation to Disturbance and Habitat Perturbation

The remarkable successes of *L. salicaria* as a worldwide pioneer is reflected in a combination of attributes that enable it to spread and thrive in disturbed temperate-climate habitats. In addition to an elaborate means of sexual reproduction and prolific seed production, *L. salicaria* has a wide scope of dispersal mechanisms. Some of these modes are adapted to long-range jumps in distribution (i.e., seeds in plumage of migratory birds); others are well suited to vegetative spread during local perturbations (adventitious shoots and roots from clipped, trampled, or buried stems, Fig. 4). Moreover, *L. salicaria*'s abundant propagules can establish themselves under a wide range of soil conditions, which enables the weed to colonize new surfaces caused by natural- or human-caused perturbations. Last, *L. salicaria*'s ability to make morphological adjustments to changes in its immediate environment (development of aerenchyma on submerged stems; change in leaf morphology with decrease in light level) enables it to adjust to a wide range of seasonal or semipermanent changes in water levels and gives it a competitive advantage against other plants growing under these conditions.

Stability of Purple Loosestrife Stands

The ability of *L. salicaria* to invade and eventually dominate North American marsh and fen communities

Table 1. *Percent frequency of occurrence of wetland species associated with* Lythrum salicaria *at 45 sites in the Northeast, Midwest, and Northwest United States and southern Canada.*

Species	Northeast (N = 15)	Midwest (N = 15)	Northwest (N = 15)	Mean (N = 45)
Typha latifolia, broad-leaved cattail	53	40	47	47
Phalaris arundinacea, reed canarygrass	27	47	60	45
Carex spp., sedge	20	27	13	20
Scirpus spp., bulrush	13	7	27	16
Salix spp., willow	0	13	20	11
Equisetum fluviatile, horsetail	0	0	27	9
Typha angustifolia, narrow-leaved cattail	13	13	0	9
Phragmites australis, reed grass	13	13	0	9
Cyperus sp., flatsedge	0	0	20	7
Alisma plantago-aquatica, water-plantain	7	7	0	5
Urtica dioica, stinging nettle	0	7	7	5
Sparganium eurycarpum, bur-reed	7	0	0	2
Agrostis gigantea (*alba*), redtop bentgrass	7	0	0	2
Acorus calamus, sweetflag	7	0	0	2
Populus deltoides, cottonwood	7	0	0	2
Chenopodium album, pigweed	0	7	0	2
Rubus spp., bramble	0	0	7	2
Euphorbia spp., spurge	0	0	7	2
Impatiens capensis, touch-me-not	0	7	0	2
Cornus stolonifera, red-osier dogwood	0	7	0	2
Convolvulus arvensis, field-bindweed	0	7	0	2
Verbena hastata, blue vervain	0	7	0	2
Solanum dulcamara, bitter nightshade	0	0	7	2
Eupatorium perfoliatum, boneset	7	0	0	2
Solidago sp., goldenrod	0	7	0	2
Aster sp., aster	0	7	0	2
Cirsium arvense, Canada thistle	0	0	7	2
Lactuca scariola, prickly lettuce	0	7	0	2
Unknown grass	0	0	7	2

is unique among our herbaceous, temperate-zone weeds. If monospecific stands of purple loosestrife were short-lived, the problem would be very much reduced; however, many stands in the Northeast have been self-replacing for more than 20 years without apparent loss of vigor. In similar habitats in the British Isles, purple loosestrife may form dense monospecies stands in areas of disturbance, but these become mixed-species stands within a few years (Shamsi and Whitehead 1974*a*). *L. salicaria*'s scattered occurrence in mixed-species stands also seems to be the usual situation in central Europe, where Bodrogkozy and Horvath (1977, 1979) studied the dynamics of mixed-species stands on the Tisza River floodplains in Hungary. Similarly, during field surveys in 1979 in seven western and southern European countries, Batra (personal communication) found *L. salicaria* growing as occasional plants in mixed-species stands. In the summer of 1984, two of the authors traveled for 8 weeks through southern, central, and northwestern Europe and Great Britain. With two exceptions, we observed *L. salicaria* to be no more than an occasional plant occupying a relict distribution in habitat remnants along ditches and waterways. The first exception was along the coastal marshes of southwestern Sweden, where individual plants became locally abundant along the disturbed upslope edges of vigorous *Phragmites australis* stands. The second exception was a monospecific stand of purple loosestrife on Weir Wood Reservoir in southeastern England. The willow-shaded borders of the reservoir had been cut in 1981–82 to create an open view of a waterfowl display area. A prolific growth of purple loosestrife dominated the site in 1983, but was already losing dominance to a vigorous resurgence of willow suckers by August of 1984.

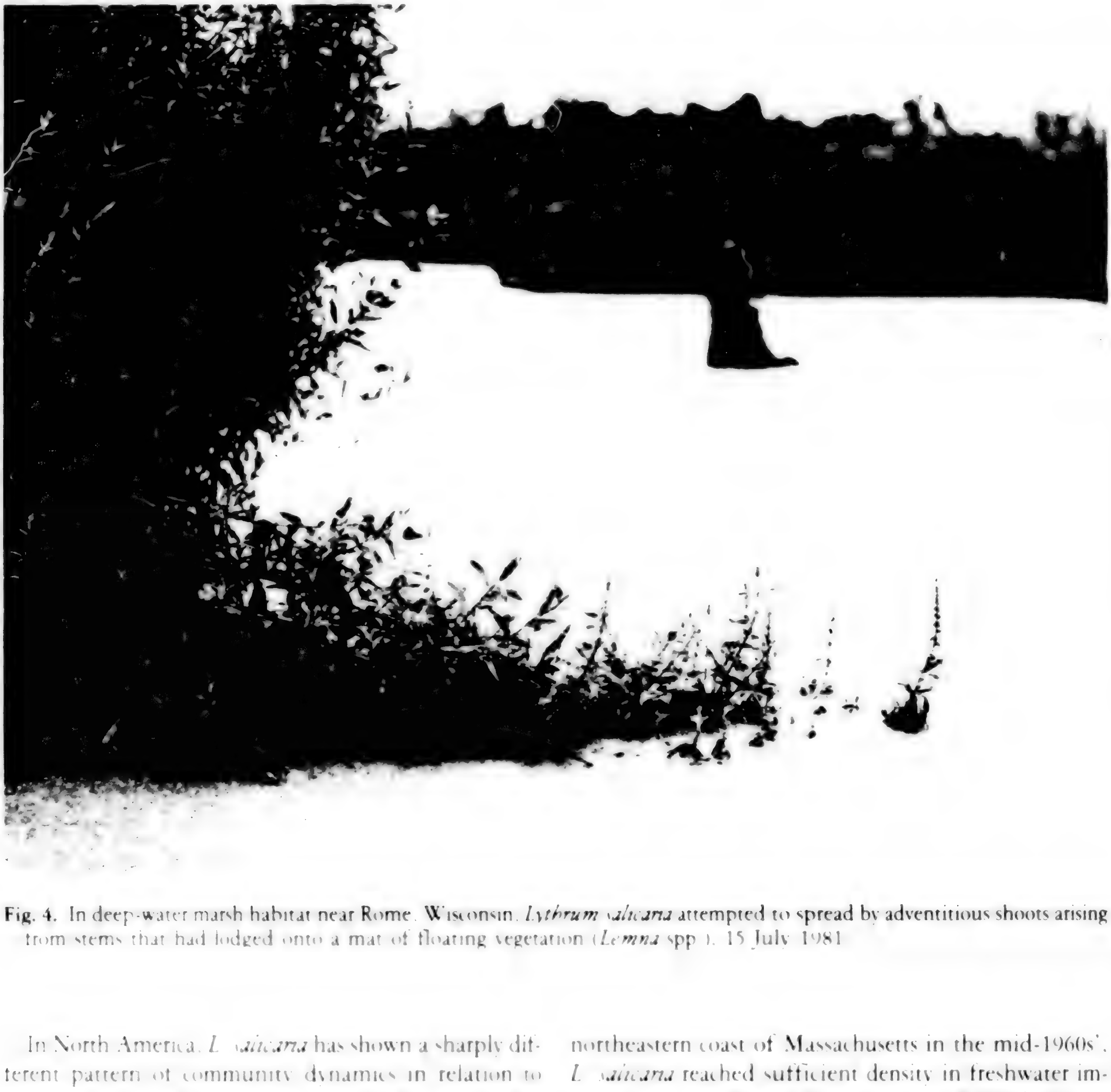

Fig. 4. In deep-water marsh habitat near Rome, Wisconsin, *Lythrum salicaria* attempted to spread by adventitious shoots arising from stems that had lodged onto a mat of floating vegetation (*Lemna* spp.). 15 July 1981.

In North America, *L. salicaria* has shown a sharply different pattern of community dynamics in relation to many of its mixed-species associates in Europe. In the late 1950's, a large percentage of 23 small wetland impoundments that had been created in the lower Hudson area of New York had become almost pure stands of purple loosestrife (McKeon 1959). As of 1980, these monospecies stands were still more or less unchanged (G. Cole, personal communication). In 1956, R. H. Smith (1964) began several years of experimental control of purple loosestrife on the Howland Island Game Management Area in central New York. Working in the same area about 20 years later, Rawinski (1982) reported that proposed water level manipulations (to enhance waterfowl habitat) had been hindered because of the threat of continued purple loosestrife infestation. On the northeastern coast of Massachusetts in the mid-1960s', *L. salicaria* reached sufficient density in freshwater impoundments on Parker River National Wildlife Refuge (NWR) to threaten their usefulness as waterfowl and shorebird habitat (H. J. O'Connor 1968, unpublished report). Despite attempts to reduce the vigor of these stands with salt-water intrusion, mowing, and other treatments, the area was still heavily infested in 1981 (G. Gavutis, personal communication).

Gilbert and Lee (1980) reported an interesting comparison of the population dynamics of purple loosestrife stands near Canberra in southeastern Australia and along coastal British Columbia near Vancouver. Both stands stretched along 500 m of lake or streamside. All plants were tallied each year to obtain style length distributions. Although the results on style length were somewhat confusing, two aspects of this study were noteworthy. First, there was very good evidence that some root crowns did not grow above ground in certain years: "in a dozen cases at Canberra and two at Vancouver, a plant was seen in one year, did not grow above ground in the next, but was present again at exactly the same place and with the same style length in the following year." Second, and germane to our present discussion, the number of plants in the Vancouver stand increased from 46 plants in 1969 to 82 plants in 1979. The results from the riverside near Canberra were altered by catastrophic flooding that reduced the initial population from 108 in 1966 to 6 in 1975. Nevertheless, recolonization returned the population to 28 in 1978, 50 in 1979, and 82 in the last year (1980) of field work.

Although we cannot evaluate their relative importance, several factors can be identified that may account for the stability of North American versus northern European stands of *L. salicaria*. First, the insect fauna foraging in North American stands is missing many key species that reduce the vigor of European plants (Batra et al. 1986). Second, although the muskrat has spread over much of Europe since its escape in Czechoslovakia in 1905 (Elton 1958), its selective foraging on *Typha latifolia* probably has a much greater impact in North American marshes where cattails are dominant compared with Europe where *Phragmites australis* is the dominant emergent aquatic. Last, with very little known of the genetics of European versus North American stocks of *L. salicaria*, we suggest that more adaptive and vigorous forms may have appeared in the North American populations.

Arrival and Establishment in North America

In introducing his "ecological chronicle" of the invasion of *Bromus tectorum* into western North America, Mack (1981) postulated four conditions that might explain the rapid spread of a transocean immigrant in its new range. Mack hypothesized that the successful immigrant may find itself "in a new homeland: (a) to which it is preadapted, ... (b) where habitat modification has occurred simultaneously with alien entry..., (c) in which its potential competitors may be inferior..., and (d) while simultaneously leaving behind in the old range both coevolved predator/parasites and competitors...." All of these ideas are worth keeping in mind as we examine the ecological chronicle of *L. salicaria*'s invasion of the North American continent.

Establishment in Maritime Northeast

The similarities in climate, soils, and glacial history between northern Europe and temperate North America have been discussed by Hultén (1972). His studies of the circumpolar relationships of many boreal plants (Hultén 1958) suggested that a species evolved on either continent is in a sense preadapted to existence in unoccupied habitats all around its potential circumpolar range. An examination of the world distributions (Fig. 2) of two of *L. salicaria*'s principal associates in North America (*Typha latifolia* and *Phalaris arundinacea*) shows remarkable parallels in distribution patterns, so much so as to suggest that in the late Pleistocene, all that was needed for *L. salicaria* to achieve circumpolar distribution was human help in crossing the North Atlantic Ocean barrier. Help was indeed forthcoming.

Modes of Establishment and Seed Sources

Although the first appearance of *L. salicaria* in North America will probably remain unknown, the colorful and showy spikes of this open-habitat plant make it probable that its presence was soon detected by early botanists. It was so well established by the 1830's that Torrey and Gray (1840) considered it to be "probably native" in their first edition of *A Flora of North America*. The continuing spread of the plant caused both authors to refer to it in later publications as probably of Eurasian origin. Stuckey (1980) documented the early distribution and subsequent spread of *L. salicaria* from annotations on herbarium collection sheets, various field notes, and published records. These historical materials offer some strong suggestions as to the sources of genetic materials and the modes of transocean transport.

Ship Ballast

Several characteristics of the ecology and distribution of *L. salicaria* in Europe favored an early immigration to North America. It was present in most of the marine estuaries of northern Europe that were the export centers to North America. Early passages from Europe were in small sailing ships carrying textiles, furniture, machinery, livestock, and immigrants to North America. Many of these vessels carried lumber, cotton, and tobacco on their eastbound return voyages (Jones 1976). These vessels required cargo or ballast (more often both) to have the necessary stiffness and trim to be sailed efficiently on their westbound passages (Bunting 1971; Le Scal 1967). Commercial cargo for American and Canadian ports was often in short tonnage, hence wrought iron, cut rock, or textiles were placed in the lower cargo holds—especially if the upper levels were fitted out to carry livestock or human immigrants. If no merchantable ballast was available, gravel, rock, rubble, or even moist sand from exposed tidal flats were laid along the keel and covered with dunnage before cargo was stowed. On arrival at their New World destination, passengers, livestock, and commercial cargo were discharged first; thereafter, ballast was hoisted and dumped. If livestock had been part of the westbound cargo, waste hay, bedding, and manure were cleaned from the holds and dumped before the ballast was lifted.

There is very little published information on the kinds of ballast used; however, Stevens (1871) advised, "Never take sand where stone is to be obtained..." and later added, "when sand is shipped [i.e., taken aboard] wet, allowance must be made for drainage by bringing the vessel well down...." Clearly, moist sand from tidal flats was frequently used as ballast and would have offered an opportunity for alien plant seeds to find their way to North American shores. The amounts of ballast taken on were considerable; Stevens (1871) recommended half of the ship's tonnage for a vessel with little cargo. Dana (1911) gave an excellent account of the discharge of ballast in 1836 at the port of San Diego. He also commented on the abuse of ballast dumping regulations by unscrupulous ship's officers: "A regulation of the port forbids any ballast to be thrown overboard; accordingly, our long-boat was lined inside with rough boards and brought alongside the gangway, but where one tubful went into the boat twenty went overboard. This is done by every vessel, as it saves more than a week of labor, which would be spent in loading the boats, rowing them to the point, and unloading them." The unauthorized dumping of ballast in shoal areas would tend to improve the chances for ballast aliens to become established.

Early American botanists were quick to pick up the arrival of Old World plants at the ballast grounds (Smith 1867; Brown 1878). A modest literature on ballast plants began to accumulate, and the term "ballast waif" came into use. Although cargo traffic far exceeded immigrant passages, the volume of immigrant traffic alone was sufficient to assure a steady flow of plant materials. Jones (1976) estimated that more than 800,000 immigrants had arrived at North American ports by 1815. The volume of traffic increased with the close of the Napoleonic wars; between 1820 and 1860, more than 5 million additional immigrants made the difficult North Atlantic passage (Brown and Roucek 1945). Even though steam propulsion was making its beginnings in the 1840's, sailing ships or steam with auxilliary sail carried most of the traffic as late as 1860. Immigration from northern Europe was not to reach its peak until 1882 (Handlin 1959); nevertheless, by the 1860's, *L. salicaria* was already well established in the maritime estuaries of North America. Later arrivals of European and Eurasian plants continued to appear on North American ballast grounds. Fourteen of the 30 *L. salicaria* sites plotted in Fig. 5 were from collections made on or near estuarine waste grounds between 1864 and 1879. In his study of the faunal connections between Europe and North America, Lindroth (1957) located and described 11 ballast sources in southwestern England that were used by sailing ships in the Newfoundland trade. Purple loosestrife was not collected by Lindroth, but three of *L. salicaria*'s North American associates (*Phragmites communis* [*australis*], *Solanum dulcamara*, and *Urtica dioica*) were listed.

Other Sources of Genetic Stock

Early botanical records indicate that other modes of arrival were also important (Stuckey 1980). Purple loosestrife was valued as an herb in northern Europe and seeds may have been brought in by immigrants. Grosse Isle, in the St. Lawrence estuary near the city of Montmagny, was one of the principal immigration centers for Canada; Rousseau (1968) cited Brunet's statement (in 1865) that *L. salicaria* had been introduced at this site by immigrants. An herbarium record from 1880 suggested purposeful introduction on a pond in Boston. There are enough other records of the escape of *L. salicaria* near gardens or cultivated sites (Washington, D.C., 1898; W. Darby, Pa., 1889; Cold Spring, N.J., 1900) to suggest that *L. salicaria* seed or rootstalks brought to North America by horticulturists were an important source of colonization.

Information on the herbarium sheets of three of the records (Stuckey 1980) plotted on Fig. 5 indicated that *L. salicaria* arrived in imported raw wool or on sheep brought over from Europe to support America's growing wool industry. American demand for raw wool began with the rapid growth of woolen mills in New England following the War of 1812 (Cole 1926). Boston became the focus of the domestic and imported wool trade. The average annual import of raw wool from 1835 to 1841 was more than 9 million pounds (Wright 1910), with France, Germany, Austria, Great Britain, Spain, Italy, and Turkey contributing fleece from most of the European range of *L. salicaria*. L. Pechuman's (personal communication) description of purple loosestrife's naturalization in the vicinity of Walkill, New York,

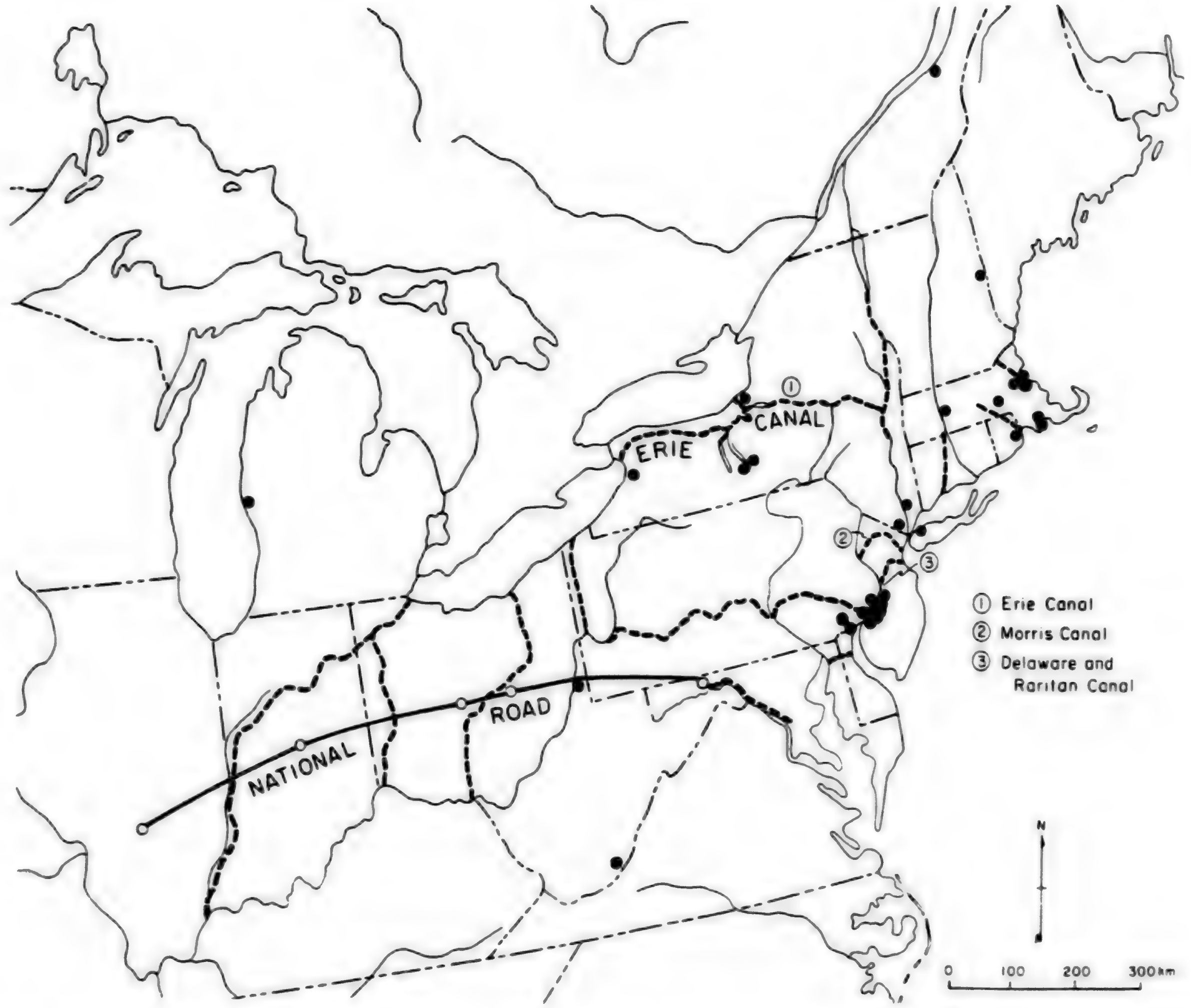

Fig. 5. Establishment and early spread of *Lythrum salicaria* by 1880. Canals in operation by 1849 are shown as dashed lines.

pointed to imported sheep as the seed source. Referring to the spread of native American plants, Martindale (1876) reported, "The large flocks of sheep brought to the Eastern market have been great distributors of those seeds which readily adhere to wool." Other references to early *L. salicaria* establishment in the vicinity of woolen mills referred to wool waste (scourings) as the source of seed (Knowlton and Deane 1921; Pellet 1944; Stuckey 1980). Salisbury (1961) considered screenings (waste) from imported wool to be a "fertile" source of alien plants in Great Britain.

In summary, it seems likely that the arrival of *L. salicaria* in North America was an often repeated event through the first half of the 19th century. This assured the inclusion of maximum temporal fluctuations in the introduced or naturalized genetic stocks. Moreover, the sources of the genetic stocks were from widely scattered habitats in northern, central, and southern Europe with climates varying from cool-moist to warm-dry. Last, the mention of several early collections as being escapes from gardens or nurseries indicates that horticultural varieties also contributed to the diversity of genetic material in North American stocks. Accepting the evidence of Halkka and Halkka (1974) of strong gene flow between island populations of *L. salicaria* in the Gulf of Finland, we can surmise that the robust populations of *L. salicaria* established in eastern North America in the 19th century had a maximum likelihood of producing vigorous and adaptive strains to exploit their opportunities on a new continent.

Chronology and Mode of Spread

Early Spread in Northeast: Pre-1880

Although *L. salicaria* was well established along the New England seaboard by the 1830's, its spread into vast stretches of interior drainage basins (Fig. 5) could not have been easily accomplished without (a) profound disturbance and stress in native wetland plant communities and (b) a ready mode of dispersal that connected marine estuaries with interior wetlands. Community stress and perturbation had its beginings in 1790 with the assignment of military lots in upstate New York to veterans of Sullivan's 1779 campaign to suppress the tribes of the Iroquois nation. In the rush of agricultural settlement that followed, wetland meadows were scythed, trampled, and grazed; upland watersheds were drastically altered as forests were cleared for cropland and pasture. A less obvious change was the cessation of aboriginal fires following early settlement. Day (1953) and Thompson and Smith (1970) documented the purposeful use of fire by Indians of the Iroquois Nation. By 1822, the effects of fire cessation were obvious to Dwight (1823), who astutely commented on the remarkable buildup of unburned surface litter in forest stands encountered along his stagecoach route through the upper Finger Lakes region. The effects of aboriginal fire on interior marshes is unknown, but the frequency of fire in these wetlands probably decreased sharply following settlement. We do not know enough of *L. salicaria*'s response to fire to judge the importance of this likely change in fire regimen.

Canals

Early canals not only provided aquatic weeds access to the interior of the continent, they also added a new source of disturbance to native plant communities. In 1817, construction of the middle section of the Erie Canal began (U.S. Inland Waterways Commission [USIWC] 1972). By the following year more than 2,000 men and as many horses and oxen were building locks, excavating channels, and smoothing adjoining towpaths (Harlow 1926). In many stretches, the canal followed upland contours that led away from natural water routes. These stretches added new seepage habitat for plant immigrants. Moreover, each canal segment required "feeders" to replace the volume of water lost in normal lock operations. Surface water diversions, flumes, and feeder canals extended into the surrounding watershed to provide an adequate water supply; profound habitat disturbance thus preceded the completion of the Erie Canal in 1825. The enormous success of the new canal was foretold in more than a half-million dollars of tolls collected in its first year of operation (Harlow 1926). In the euphoria of expectations that followed the opening of the Erie Canal, more than 4,800 km of canals were constructed by 1840 in New England, New York, Pennsylvania, New Jersey, and Ohio (Tanner 1970). The most important of these water routes are shown on Fig. 5. Careful examination of the early *L. salicaria* plots shows that with the exception of the interior Pennsylvania canals, the spread of purple loosestrife was closely related to canal traffic moving inland from the northeastern marine shipping estuaries. Twenty-seven of the 30 collection localities were near seaports or along canals. Despite the abundance of early records along the Delaware and Raritan Canal, the invasion of Pennsylvania, Maryland, Virginia, and West Virginia was very slow compared with the invasion of upstate New York along the Erie. The greatest concentration of *L. salicaria* establishments was along the Delaware and Raritan Canal and the Erie Canal. Several factors may account for the sharp differences in spread. First, these canals were low profile waterways that offered direct connection between seaboard and interior. In 68 km, the D&R Canal needed only 14 locks and 35 m of lift to connect Raritan Bay with the Delaware River. The Erie Canal needed only 83 locks in 616 km to lift its barges from the Hudson River over a 192-m summit on their transit to Lake Erie. In contrast, canals leading into the interior of Pennsylvania were confronted by the mountainous northeast–southwest ridges of the Appalachian Region. The Morris Canal had to climb from sea level to a summit of 279 m before dropping 230 m into the upper Delaware River at Phillipsburg. Twenty-three inclined planes were needed to winch the barges overland from one watershed to the next, thus breaking the water connection between each segment. Second, in contrast to the broad, open glacial basins of upstate New York, the interrupted waterway segments in Pennsylvania moved along relatively narrow valleys with thin, early-drift mantles and well-shaded stream margins. All of these factors would have been deterrents to the spread of an emergent aquatic plant.

Other Routes of Early Spread

The National Road, various turnpikes, and regional railroad networks were also important routes for the westward expansion of the new republic. The National Road (Fig. 5) reached the Indiana line by 1840 (Ohio Writers' Project 1940); however, despite heavy wagon traffic over the route since its beginnings in 1811 at Cumberland, Maryland, it was of little importance as a means of *L. salicaria* spread. The single establishment of *L. salicaria* reported from the bottomland of the Ohio

River at Wheeling, West Virginia, in 1878 might well have arrived with river traffic. The first railroad connection between Chicago and the eastern seaboard came into service in 1852 (Meyer 1969); railroad tonnage surpassed canal tonnage in New York and increased steadily to more than 3 times the tonnage of canals in 1880 (USIWC 1972). Nevertheless, an inspection of railroad routes and *L. salicaria* collection plots shows little correspondence. This is not surprising; railway rolling stock and cargos are a possible but not very likely mode of spread for an aquatic weed. Most railway trackage is well drained and crosses wetland habitats on raised embankments. Moreover, railroad rolling stock seldom comes in contact with purple loosestrife seed sources. *L. salicaria* rarely occurs in seed or grain cargos, although it could have gained access in marsh hay used as feed or bedding for livestock. Last, although livestock shipments on midwestern railroads began to reach significant tonnages after 1850, regional railroad networks were built out from centers that they served. Traffic flow into the Chicago hub came mostly from purple loosestrife-free areas in the adjoining midwestern States and the Great Plains.

In summary, all evidence suggests that the early phase of spread of *L. salicaria* into the interior of North America was by waterborne commerce into recently disturbed or stressed habitats. Finally, although some of the new establishments were probably escapes from cultivation, more than three fourths of the records indicated fortuitous or accidental spread from other sources.

Spread into Midwest: 1880–1900

Figure 6 includes the 30 collections shown in Fig. 5 along with the localities of 40 new collections made between 1881 and 1900. From 1800 to 1900, canal traffic declined and railroads not only took over all priority shipments but made severe inroads into the bulk cargo (coal and grain) that had once brought the principal revenues to canal carriers. Most of the regional and continental railroad networks were established in this period. Yet, despite the tremendous expansion of rail traffic, little additional spread in *L. salicaria* (Fig. 6) can be related to traffic on the new rail networks. Most of the

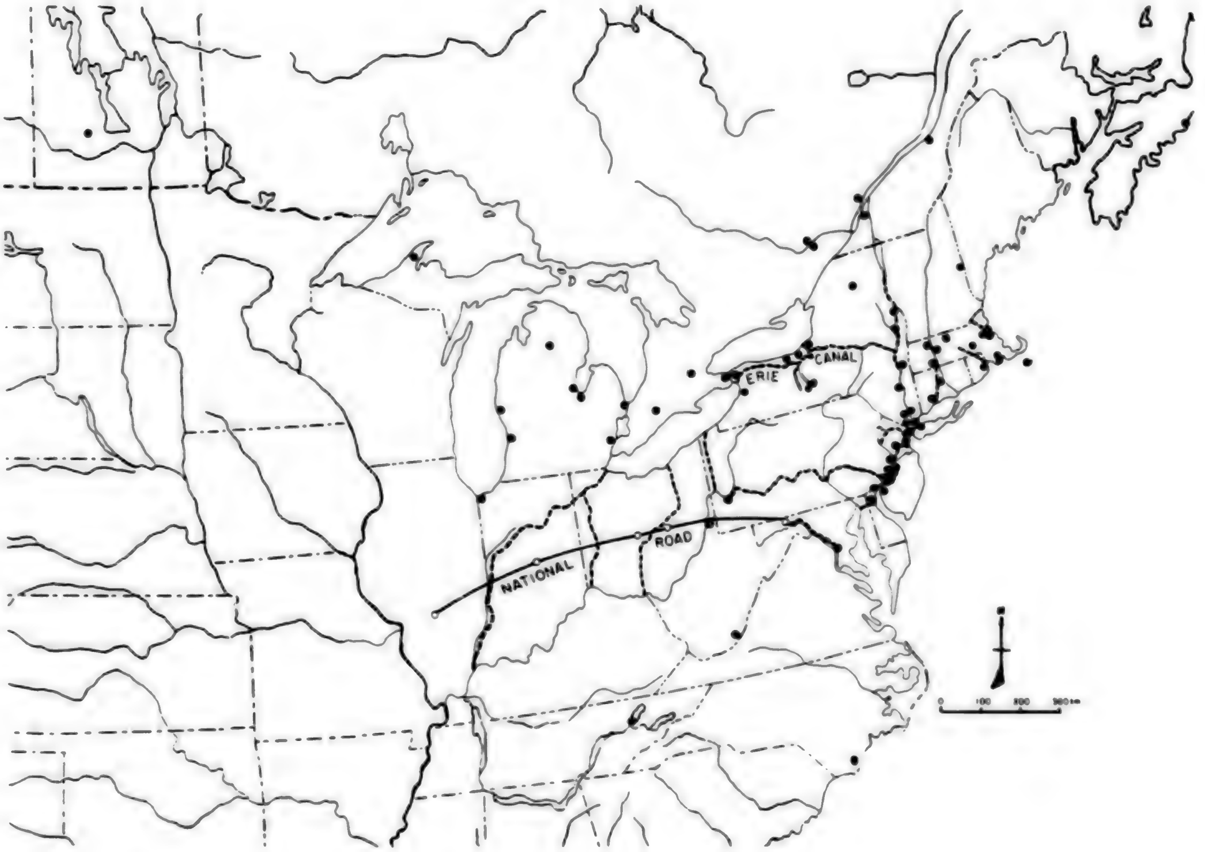

Fig. 6. Spread of *Lythrum salicaria* as of 1900 (after Stuckey 1980).

new records of *L. salicaria* establishment occurred along marine commerce routes or at coastal or inland ports. From 1880 to 1900, maritime traffic was very active from Buffalo to ports on the Great Lakes. Immigrants, livestock, and cargo were transferred from the Erie Canal terminus at Buffalo to sailing schooners and steamers for transshipment into the midwestern frontier. The collection site in Michigan is at Muskegon Harbor—an early lumber port.

Colonization of Midwest and Northwest Pacific Coast: 1901–1940

The continued spread of *L. salicaria* during the first four decades of the 20th century is shown in Fig. 7. New records were reported from maritime States and Provinces of the Northeast. Coastal sites in eastern Maine, western Nova Scotia, the Gaspé Peninsula, Anticosti Island, and Newfoundland were colonized by *L. salicaria* by 1940. Coastal schooner trade in lumber, coal, grain, and hay was very active early in this period and may have been responsible for the spread of *L. salicaria* from colonized areas to unoccupied estuaries. For the first time, establishments were reported from marine estuaries in the Pacific Northwest, suggesting again that marine commerce was the principal mode of spread.

The early 1900's saw the last struggles of a declining and obsolescent canal network. In New York, the shipment of grain shifted from 96% by canal in 1868 to 82% by railroad in 1906 (USIWC 1972). Two transcontinental railroad routes in Canada and six in the United States were in operation for most of this period, but contributed only a few new records of *L. salicaria* spread. The construction of our first State and Federal highway networks occurred during this period with seemingly little effect on the spread of purple loosestrife.

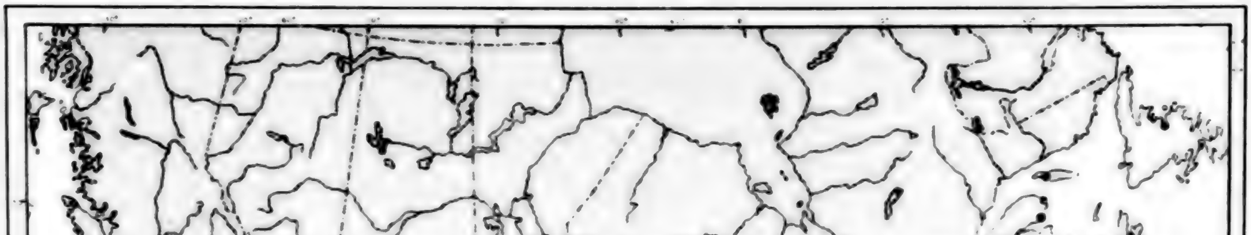

Fig. 7. Distribution of *Lythrum salicaria* as of 1940 (after Stuckey 1980). Stipple pattern indicates extent of Wisconsin Age glacial drift.

Spread into the Arid West: 1941–1985

L. salicaria's known distribution as of 1985 (Fig. 8) shows a greatly expanded range since 1941. In the Northeast, herbarium specimens were obtained for the first time from New Brunswick and Prince Edward Island. Eastward range extension was also obvious on both sides of the St. Lawrence estuary. Colonization of the northern Midwest was now nearly complete with range extensions occurring in western Minnesota. New locations also appeared in the upper Red River Valley along the Minnesota–North Dakota border and extended across the international border into Manitoba and the wetlands of Lakes Winnipeg and Manitoba. But the most dramatic colonizations since 1940 occurred in interior western North America where *L. salicaria* infestations appeared in an additional 12 States and 2 Canadian Provinces lying west of the 100th meridian—Powell's (1962) definition of the eastern boundary of the Arid West. With the exception of the Arkansas and Colorado rivers and the Rio Grande, all of the major watersheds within this vast expanse had now been colonized. Vigorous new colonies in California, Idaho, Nebraska, Wyoming, and Washington suggest that *L. salicaria* may become troublesome in the wetlands of the Arid West.

Two major public works programs contributed to massive habitat changes that favored purple loosestrife spread in western States. The idea of using the abundant water sources of the western cordilleras to irrigate outlying steppe or desert benchlands had its roots in the life and work of John Wesley Powell. These concepts took form as one of Theodore Roosevelt's legislative priorities and gave rise to the Federal Reclamation Act of 1902. At this time the total number of hectares under irrigation (Fig. 9) on Federal projects was about 8,000. By 1910, the efforts of the newly formed Reclamation Service had increased the total number of hectares under irrigation by more than 20-fold to 192,000. Rapid growth continued through the next 20 years to about 1,100,000 ha in 1930. Shortly thereafter, Reclamation received a

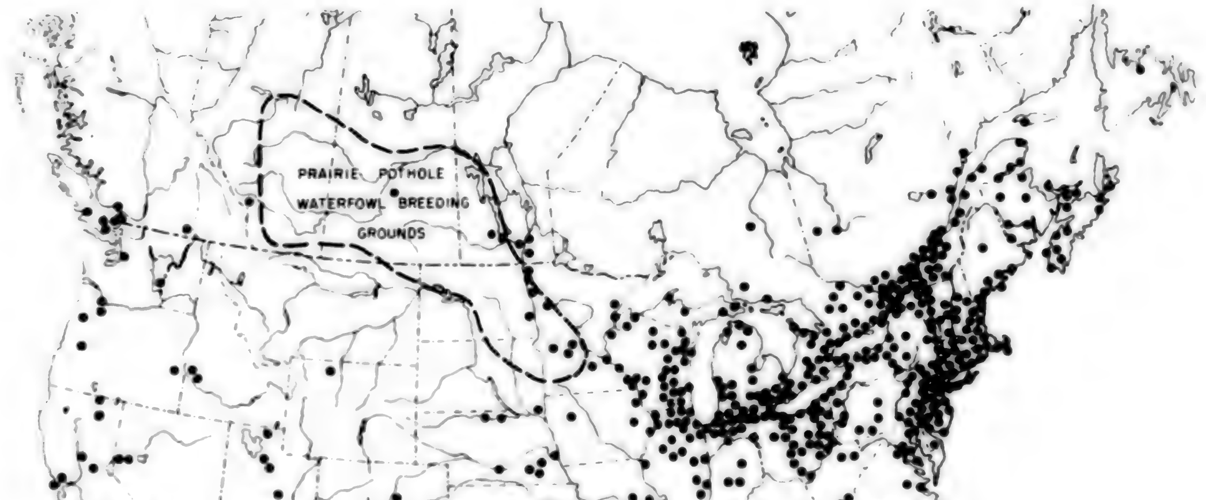

Fig. 8. Distribution of *Lythrum salicaria* as of 1985.

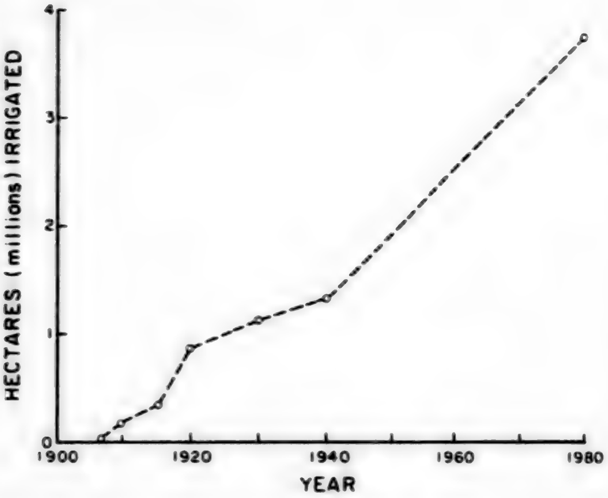

Fig. 9. Hectares (in millions) of land under irrigation on Federal Reclamation Projects from 1906 to 1980; the 1980 estimate is projected from indices of irrigated acreage on Federal Reclamation Projects 1956–1978 (U.S. Water and Power Resources Service 1979).

vigorous boost from Franklin D. Roosevelt's New Deal, and new projects were established that eventually pushed the irrigated hectares through a threefold increase to about 3,800,000 by 1980. Although most irrigated land is in cultivated crops and therefore probably not susceptible to invasion by purple loosestrife, off-water swales that collect runoff from irrigated fields, and seepage slopes along canals and ditches, are likely places for *L. salicaria* encroachment. The recent infestations in California, Idaho (Fig. 10), Washington, and Wyoming (Fig. 11) are all in irrigation areas. Chemical control has already been necessary in irrigated rice in California (Howell and True 1966) and in a seepage pasture west of Boise in Ada County, Idaho (W. Hartman, personal communication).

Called the largest public works project in United States history (Leavitt 1970), the national superhighway network has resulted in 97,000 km of road construction at an average cost of $930,000 per km. Specifications for the interstate system called for well-drained crowns; the low gradients of even the steepest hills were achieved with massive excavations and backfills. The excavations often cut through local groundwater seams and created new habitat for emergent aquatic plants. These moist areas are usually first colonized by *Typha* spp. and other native aquatics. More recently, many of these seepages have been invaded by purple loosestrife, perhaps from seed transported by highway traffic.

H. Brumsted (letter, 22 August 1978) described the status of purple loosestrife along I-84 between Danbury, Connecticut, and the junction of State highway 17, near Middletown, New York. He noted, "as expected, *Lythrum* was present in all types of depressions associated with the highway. . . . What I did not expect to find, however, were single clumps and scattered colonies of *Lythrum* amid areas of grass on the median, and also on fill slopes, that certainly were not ditches or wet depressions. . . . [what] surprised me most . . . was [*L. salicaria*] growing at the left edge where pavement joined the median. . . . during the return trip on the 21st, I had opportunity to observe the effect of a trailer truck's passing . . . one roadside clump of *Lythrum*. . . . The truck, passing at about 65 mph at my left, caused a partial vacuum . . . that caused a clump of *Lythrum* at the median edge of the pavement to bend over the road at what appeared to be an angle of at least 45 degrees. Were this to occur when *Lythrum*'s capsules were dehiscent, it would seem virtually certain that seed would be swept into the air currents and onto the highway. I see this . . . as a primary means by which the minute seeds of *Lythrum* could . . . be transported great distances." In addition to suggesting the role of superhighways in creating newly disturbed habitat that enlarges the opportunities for weeds, Brumsted pointed out that whereas earlier highways followed the ridges and valleys of the Appalachian region, the superhighways cut through them and thereby broke open the barriers that had previously blocked the spread of purple loosestrife into the next watershed.

Rate of Spread

Mack (1981) and Forcella and Harvey (1983) used herbarium specimen records and reports of field collections or observations as a means of estimating the rate of spread of rangeland weeds. Although plant collection records have many limitations as indicators of abundance, they are useful as records of occurrence. Several assumptions must be met before the value of these sources can be accepted: (a) a reasonably uniform level of field activity must carry through the span of the collections, (b) the field activity must occur in a more or less random pattern over all of the collection area, and (c) the plant must be easily seen and identified. Of the first assumption (a), by the early 1800's, botanical field collections were well under way in eastern North America; John Torrey and Asa Gray published the first volume of their projected *A Flora of North America* in 1840. Moreover, their efforts were vigorously supplemented by colleagues at other institutions and by private collectors—often medical doc-

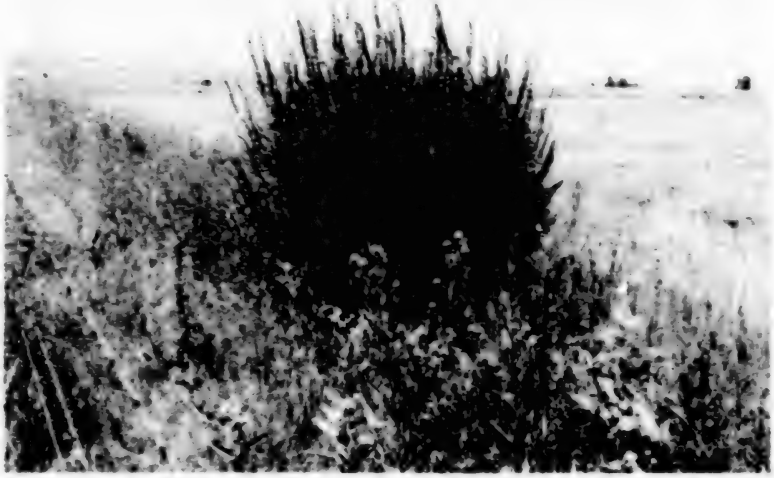

Fig. 10. A mature and robust purple loosestrife plant (height 2 m, width 1.5 m) grows in an "off-water" ditch in an irrigated hay meadow 10 km west of Boise, Idaho, 16 July 1980.

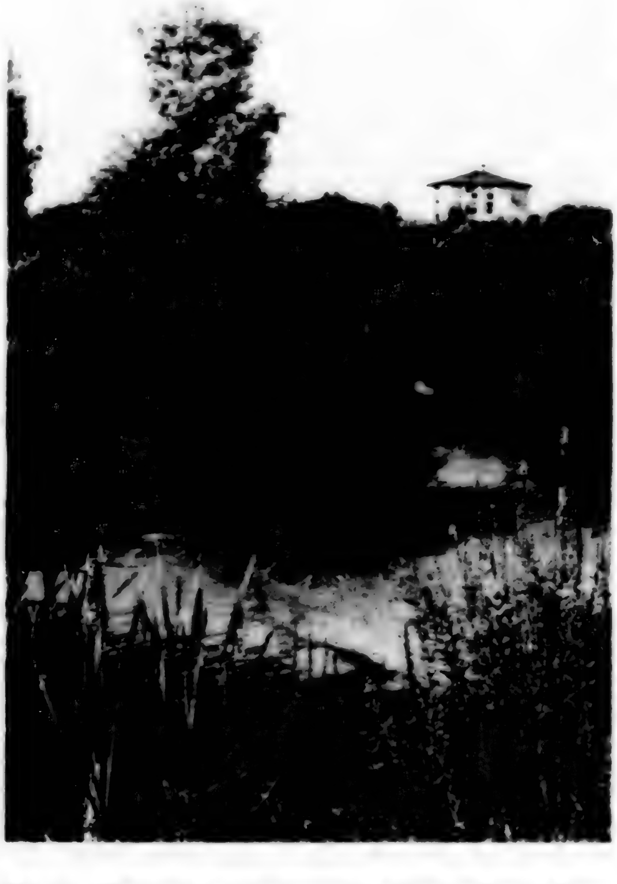

Fig. 11. Wyoming's only reported *Lythrum salicaria* infestation has invaded a once-thriving stand of *Typha latifolia*, 6 km southwest of Powell, Wyoming, 27 August 1982.

tors (as were Gray and Torrey), whose interest in botany may have stemmed from training in herbal medicine. A dozen or more academies and natural history or scientific societies published the records of field collections by this network of enthusiastic but highly competent amateur botanists. If the era of contributing amateur botanists diminished with the turn of the century, their collecting efforts were replaced by trained botanists at newly established private and public institutions. It is less certain that all of the collection range (b) has been evenly covered in a random pattern. This assumption seems to be reasonably met in early collections, but once a species became well represented in an herbarium, the level of collecting effort declined (Stuckey 1980, Table 1), making an estimate of the frequency of encounter less sensitive. Last (c), the tall and colorful inflorescences of purple loosestrife are dramatically obvious and identification is quite straightforward.

We divided four States (New York, Michigan, Wisconsin, and Minnesota) into 15′ latilong blocks and scored the cumulative occurrences of distribution from 1860 to 1980 (Fig. 12). These States have similar climates and vegetative zones, a common history of Pleistocene glaciation, and an abundance of open glacial marshes—habitat that is highly susceptible to invasion by purple loosestrife. A latilong block has an area of 771.7 km^2; 1,172 blocks make up the area of the four States. Several generalizations are obvious in the configuration of the data points. Purple loosestrife's rate of spread has been slow compared with the invasion of the western range by cheat grass, *Bromus tectorum* (Mack 1981); however, within 20 years

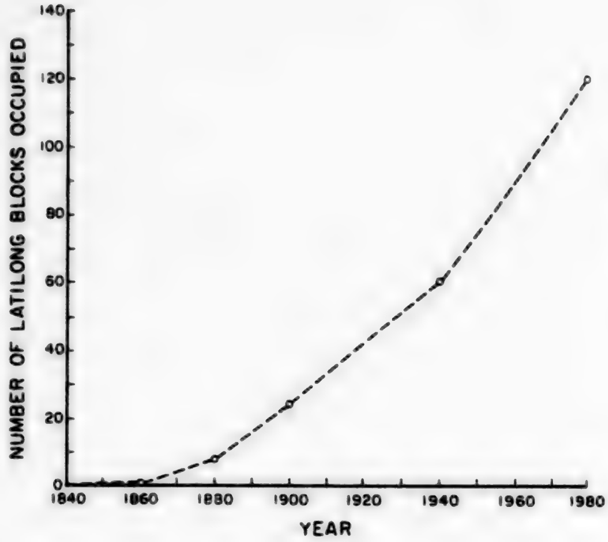

Fig. 12. Number of 15′ × 15′ latilong blocks occupied in westward spread of *Lythrum salicaria* through New York, Michigan, Wisconsin, and Minnesota from 1840 to 1980. *N* total blocks = 1,171; area each block = 771.7 km^2.

of its first report in the southern Hudson Valley in New York, purple loosestrife had begun a pattern of geographic spread that indicated a high degree of preadaptation to North American habitats. The infestation of native habitat has been increasing exponentially since 1880, with a sharp upturn in the rate of spread beginning in 1940. From 1900 to 1940, the rate of spread was roughly 1 latilong block per year; from 1940 to 1980, the rate increased to 1.5 latilong blocks per year. It could be argued that the sharp increase in *L. salicaria*'s rate of expansion is as much a measure of pervasive habitat disturbance as of the aggressiveness of the weed. The extent of habitat disturbance, including various enhancement plans for improving the productivity of wetlands, has been, and continues to be, parallel to the exponential increase of our human population. Plots of human impact on the North American environment, that is, energy consumption, wastes created, acres cultivated, volume of water impounded, highway mileage, chemicals and fertilizers used—all would approximate an exponential curve.

Purposeful Introduction

Most of our early records of *L. salicaria*'s spread into the estuaries and canals of northeastern North America indicate accidental transport in ship ballast or in imported wool. Nevertheless, purposeful introduction could have occurred at a very early time and has become an increasing problem in the recent history of spread.

Purple Loosestrife as an Herb

Some of the early escapes of *L. salicaria* could have been from herb gardens that were established with seeds imported from northern Europe. Stevens (1961) referred to the long history of use of *L. salicaria* for healing. He quoted Dioscorides (1st century) as the earliest authority, who reported, "The herb is tart and strong in taste, of an astringent and refrigerant nature, good for stanching both outward and inward bleeding; sap extracted from the leaves and drunk stops blood-spitting and dysentery, and sour wine in which the leaves have been boiled when taken internally will have the same effect; and if the plant is set afire it gives off a pungent vapor and smoke that drives away serpents; and flies cannot stay in a room where this smoke is." In describing the medicinal properties of various Lythraceae, Pammel (1911) said, "Tannin occurs in the root of *Lythrum Salicaria*." In 1916, Kraemer (as have other authors) referred to the generic name *Lythrum* as being derived from the Greek word for blood "perhaps because of its [loosestrife's] styptic properties." Similarly, Altschul (1973) quoted Scringe's reference to *L. salicaria* as "Herbe astringente, faible." More recently, Grieve (1959) noted that although *L. salicaria* is now seldom used, it was highly recommended in early herbals. Powders were made from dried leaves and decoctions from the roots. These were used to treat chronic diarrhea and dysentery, as well as leucorrhea and "blood-spitting." Green or dry leaves were also used to heal wounds, ulcers, and sores. Describing human use of this herb in Palestine, Zohary

(1972) said, "The young leafy shoots are eaten as vegetables; the flowering branches are used in folk medicine to prepare astringents, tonics and styptics."

The careful cultivation and almost intimate settings of herb gardens would make them unlikely sites for the escape of *L. salicaria*. Nevertheless, as we indicated earlier, this may have been the origin of some of the early establishments along the eastern seaboard. With the rise of modern medicine, the declining interest in medicinal herbs has made the herb garden an unlikely factor in the spread of *L. salicaria* across North America.

Horticultural Escapes

The profuse and attractive floral displays of purple loosestrife have made the plant well known to gardeners throughout the world. Its use in Europe probably extends back into the Middle Ages; however, confusion between *Lysimachia* and *Lythrum* in early garden books makes lists of plants used somewhat uncertain (Turner 1548 *as cited in* Grigson 1955). Nevertheless, by the time purple loosestrife was being introduced or becoming naturalized in North America, Sweet (1839) said of *Lythrum*, "will thrive in garden soil...all are readily increased by dividing the root...." Similarly, the British Annals of Horticulture (Anonymous 1847) listed *Lythrum salicaria* as "a plant of great beauty.... never to be omitted from the banks of a piece of water." Buist (1852), in an American flower garden directory, listed *L. alatum*, *L. virgatum*, *L. diffusum*, *L. roseum*, and *L. lanceolatum* as species that will grow well if given adequate light. Of these species, Bailey and Bailey (1976) referred to *L. roseum superbum* as one of many horticultural varieties of *L. salicaria*. In a text on garden botany, Gray (1869) noted that *L. salicaria* was not uncommon in old gardens. Last, referring to old gardens in Virginia, Boggs (1932) included *L. salicaria* as one of many plants derived from English gardens of the 17th, 18th, and early 19th centuries. Clearly, *L. salicaria*, or one of its horticultural varieties, was present in early American gardens and may have been a source of early escapes.

The inclusion of *L. salicaria* in garden and border plantings has continued throughout Canada and the United States. Several large nurseries have developed their own horticultural stocks, including strains claimed to be infertile. We have observed several relatively fragile garden *Lythrums* (source unknown) that did not produce seeds or capsules. Various cultivars of *L. salicaria* are shipped as rootstocks. In the West, at least two national retail companies currently offer *L. salicaria* stocks (some of them hybrids) as potted plants. Seedlings or segregates of these stocks continue to be important sources of regional and local spread in the expanding range of purple loosestrife.

Naturalization as a Honey Plant

British beekeepers were aware of the attractiveness of purple loosestrife flowers to bees (Grieve 1923); however, it was only 1 of 18 wild plants mentioned by Mace (1976) as a supplemental source of nectar and pollen in Great Britain. Although American beekeepers show more enthusiasm for purple loosestrife than do Europeans, Pellet (1947) did not include *L. salicaria* among wild plants of major importance as nectar and pollen sources in North America. He described purple loosestrife as "...the one plant which can be planted with confidence in boggy spots...." A query in the February 1944 issue of the *American Bee Journal* (Anonymous 1944) described the abundance of *L. salicaria* along the Merrimac River in Massachusetts and asked about its rank as a honey plant. Subsequent contributions to the *American Bee Journal* from Iowa (Pellet 1944), British Columbia (Van't Haaff 1968), Minnesota (Bunch 1977*a*), and New York (Hayes 1979) traced the growing interest in purple loosestrife as a honey plant. An apicultural supplier in the Midwest has offered purple loosestrife seed for sale, and instructions for "naturalizing" the plant have been published (Pellet 1956). The role of beekeepers in contributing to the spread of purple loosestrife is difficult to evaluate, but clearly, their efforts to "naturalize" purple loosestrife could account for many of the recent extensions of the species in the Midwest and Far West. Moreover, their efforts have not been wholly irresponsible. One honey plant enthusiast (Mead 1957) included five criteria for prospective honey plants, one being "...any danger of its becoming an offensive weed." The *American Bee Journal* also published a letter (Hughes 1977) and a press release (U.S. Fish and Wildlife Service [USFWS] 1979) that described the threat of purple loosestrife to wetland habitats.

Other Sources of Escapes

The last 30 years have seen the growth of a healthy and steadfast interest in the preservation of native habitats. A corresponding rise in investments in weekend cottages and the restoration of natural habitats on some of these properties has taken place. This concern has also influenced city, county, and State efforts in establishing nature preserves for the education and enjoyment of all age groups. In response to the needs of landowners or preserve managers for seed, 160 companies offer seed mixes of "wildflowers" and native prairie herbs and grasses (Wade 1985). Wade (personal communication) examined lists of species offered by more than 50 of these seed outlets and found that about 25% of the native-plant seed mixes contained alien species; 10% of the lists with alien seeds included *L. salicaria*. The inclusion of purple loosestrife in these seed mixes is a serious threat to regional and local habitats that have thus far escaped infestations by this alien. Indeed, prairie wetland restoration with some of these mixes would be an open invitation to habitat degradation by the dominance of purple loosestrife.

Potential Spread

Although we do not know enough about *L. salicaria*'s growth requirements or genetic plasticity to make an accurate forecast of the limits of its spread in North America, some reasonable projections can be made from examining its spread throughout the world. The worldwide distribution of *L. salicaria* clearly identifies it as a plant of temperate climates with a strong affinity for moist or saturated soils. The northern limits of *L. salicaria*'s distribution in Europe (Fig. 2) and the experimental work of Shamsi and Whitehead (1974*a*, 1974*b*, 1977*a*, 1977*b*) indicate that purple loosestrife will be a vigorous competitor with native American flora throughout the marshes and alluvial wetlands of the northern United States and southern Canada.

Eastern Seaboard

By 1900 (Fig. 6), purple loosestrife was established along the eastern seaboard as far north as Nova Scotia and as far south as North Carolina. The infestations in Nova Scotia have continued to spread slowly but have not shown the vigor of more southerly establishments. The plant may not have reached its ultimate northerly distribution, but its rate of spread has slowed markedly in comparison with its continued rapid expansion into western North America. Similarly, the early establishment on the Cape Fear estuary (near Wilmington, North Carolina) has been static, if indeed it has survived. Radford et al. (1964) did not mention *L. salicaria* in the Cape Fear area, but described the plant as very rare in marshes in northeastern North Carolina (Watauga County). Again, neither *T. latifolia* nor *P. arundinacea* has been a successful plant as far south as North Carolina. Furthermore, despite the early establishment of *L. salicaria* on the Delaware River ballast grounds, purple loosestrife has not been successful in invading disturbed coastal marshes in New Jersey. From the Hudson River estuary southward, reed (*Phragmites australis*) dominates fresh to brackish marshes. The presence of this vigorous competitor may, in part, explain the failure of *L. salicaria* to invade southern coastal wetlands.

Midwest

Purple loosestrife's obvious success in displacing cattail inside the limits of Wisconsin glaciation (Fig. 7) marks it as a serious threat to wetland habitats throughout the glacial basins and riparian wetlands that are the primary producers of waterfowl and other marsh wildlife in the Atlantic and Mississippi flyways. Shaw and Fredine (1956) defined eight types of inland fresh wetlands in their assessment of wetlands of the United States. Purple loosestrife has been highly successful in colonizing at least three of these types: Type 2—Inland fresh meadow; Type 3—Inland shallow freshwater marsh; and Type 4—Inland deep freshwater marsh. The area estimates by Shaw and Fredine of these three wetland types in the seven north-central States exceed 1.4 million ha (3.6 million acres). More than 90% of these wetlands would fall within the boundaries of the Wisconsin glacial drift line and are highly susceptible to degradation from *L. salicaria* invasion.

West of 100th Meridian

The potential threat of purple loosestrife invasion in prairie pothole wetlands of North Dakota, South Dakota, Manitoba, and Saskatchewan is difficult to evaluate at this time. The plant has been unable to invade saline wetlands in New York State's lower Hudson and Long Island areas; this strongly suggests that *L. salicaria*'s growth is somehow inhibited by high soil conductance. Similarly, *L. salicaria* faces a gradient of salinity as it invades new habitats west of the 100th meridian. Nevertheless, the recent report (Thompson and Yates 1985) of an infestation in an off-water swale near Powell, Wyoming, indicates that purple loosestrife will be troublesome in prairie wetlands of pH 7.5 or less and able to invade but not dominate open habitats with soil pH values up to 8.0. The Garrison Project in North Dakota lies in a critical position across this zone of neutral to alkaline soils. Purple loosestrife is already established east and north of the project, but has not been reported upstream from Garrison Dam.

Habitat Vulnerability

Wetland and riparian habitats vary greatly in their resistance to invasion by *L. salicaria*. Since natural spread of purple loosestrife is primarily by floating seeds or propagules, the continuity and configuration of a watershed strongly influence the rate and ease of expansion of a local infestation. Isolated wetland basins (as in northern prairie potholes) are relatively secure from the spread of seeds or propagules of purple loosestrife, whereas wetland complexes connected by a common waterway (e.g., the Mohawk waterway in upstate New York, Upper Mississippi navigation pools, and the Klamath River wetland complex in Oregon) are highly susceptible sites. The gradient and cross-section of a stream also strongly influence its resistance to *L. salicaria* infestation. Mountain or high plateau streams with steep gradients and narrow canyons (e.g., Snake River in Oregon, the Colorado River in Colorado, and the Wind River in Wyoming) are frequently scoured, with few eddies or slack-water areas where emergent aquatic plants can take hold. In contrast, low-gradient streams with broad alluvial deposits offer many sites for wetland plants to colonize and are susceptible to purple loosestrife infestation and spread. Many streams have shade-covered banks (riverbottom hardwoods in the East; spruce, willow, and alder borders in many western streams) where the high light requirements of *L. salicaria* seedlings preclude development and make these sites unsusceptible to invasion.

The vulnerability of a habitat to invasion by *L. salicaria* can be judged from the occurrence of its most frequent plant associates (Table 1). The presence of cattails, reed canarygrass, sedges, or rushes in marsh basins or along riparian wetlands identifies a habitat that can be invaded by *L. salicaria*. Last, one of the most important influences on the security of habitats against invasion by alien species is the degree of disturbance or environmental stress suffered by its soil, water, and biota. In the Midwest, Auclair (1976) estimated that 92% of the original prairie (upland) surface was converted to a cropland–temporary pasture system between 1833 and 1934; during the same period, 66% of the original marshlands were "transformed." In the subsequent 50 years, the widespread and pervasive effects of soil, water, and air pollution suggest that no wetlands have escaped some form of perturbation.

Impact of *Lythrum salicaria* on Wetland Habitats and Wildlife

Although we need quantitative measurements of the effects of various stages of *L. salicaria* invasion on the structure, function, and productivity of North American wetland habitats, the replacement of a native wetland plant community by a monospecific stand of an exotic weed does not need a refined assessment to demonstrate that a local ecological disaster has occurred. Nevertheless, a summary of existing information is needed. McKeon (1959) reported that a large percentage of shallow impoundment marshes in the lower Hudson area of New York had become solid stands of purple loosestrife and were thereby degraded as waterfowl production sites. In upstate New York, L. S. Smith (1959) noted that, with age, invading *L. salicaria* ultimately dominated wetland habitats with tall, dense, brushlike stands that were impenetrable to boats. These stands also excluded desirable waterfowl food plants (Fig. 13). R. H. Smith (1964) later reported *L. salicaria*'s impact on New York marshes as, "in the wildlife marsh, with average water depths of 12 to 18 inches, purple loosestrife can take over and occupy much water area that should be occupied by waterfowl food plants." Similarly, Friesen (1966) reported on the replacement of native food plants for ducks and geese in Delta Marsh, Manitoba, by *L. salicaria*. At the Montezuma NWR in New York, Rawinski and Malecki (1984) used line transects through adjacent stands of emergent purple loosestrife and cattail to measure wildlife usage. They found that muskrats and long-billed marsh wrens (*Cistothorus palustris*) used cattail stands almost exclusively, whereas red-winged blackbirds (*Agelaius phoeniceus*) clearly preferred purple loosestrife.

History of a Waterfowl Impoundment

The history of the encroachment of purple loosestrife into a waterfowl impoundment in central New York offers many insights into the potential impact of this weed in wetland habitats. In 1965, an experimental greentimber impoundment was established on the Montezuma NWR in a tract of muck–hardwood timber lying at the north end of Lake Cayuga (Haramis and Thompson 1984, 1985; Thompson et al. 1968). The forest floors of two adjacent 125-ha units were impounded with spring runoff water to a mean depth of 35 cm to encourage waterfowl nesting. These shallow waters were withdrawn in July or early August to relieve the forest community from possible water stress. Both experimental impoundments were compared with a 125-ha control area that remained undisturbed.

Dikes and ditches that carried water on and off the forest floor were constructed with a shelflike berm that was intended to surround the forest units with a ring of

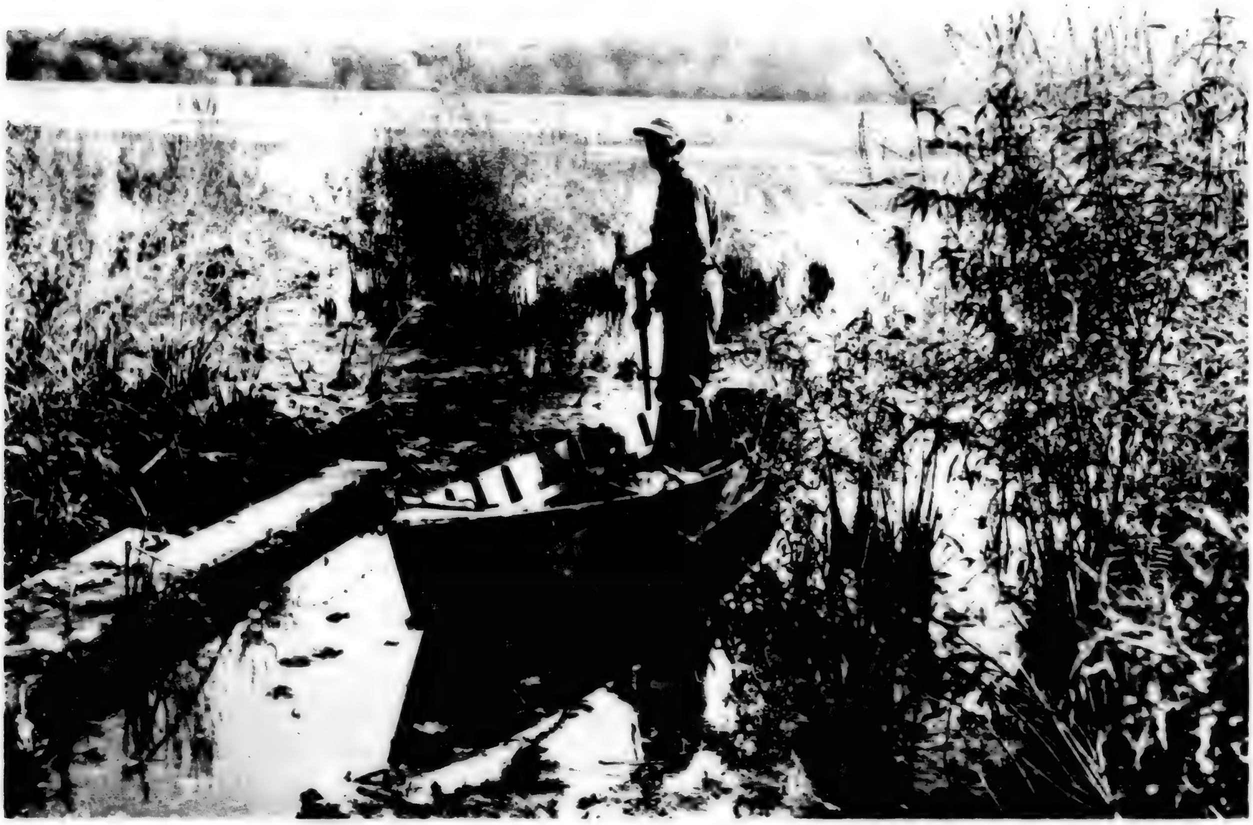

Fig. 13. Purple loosestrife has displaced native emergent cover in front of this private shooting club in upstate New York, 3.2 km west of north from Savannah, 18 October 1968.

emergent and floating aquatic vegetation. This peripheral zone was to serve as foraging area and escape cover for broods reared in the flooded timber. In the first year of operation (1965), cattails (*Typha latifolia*) colonized the rims of all of the ditches. In the second year, cattails continued to spread along the impoundment water line, while the shallow berm area developed an ideal mix of open water with floating plants (*Potamogeton* spp., *Utricularia vulgaris*, and *Lemna minor*) and emergent aquatics (*Alisma plantago-aquatica* and *Acorus calamus*). Meanwhile, waterfowl—primarily wood ducks (*Aix sponsa*) and mallards (*Anas platyrynchos*)—were nesting in natural tree cavities and on wind-throw mounds in densities of about one pair per hectare. Although early monitoring of the green-timber impoundment units indicated that these forest communities were adjusting to the new water regimen, purple loosestrife appeared along the impoundment rims in the second growing season (1966). The encroaching seedlings took root along the strand of mean full-pool line, suggesting water distribution of floating seeds or propagules. Beginning in 1966, we made biennial estimates of the percentage of green biomass made up by purple loosestrife along the dike slopes facing the east and west impoundments. By 1968, purple loosestrife had become widely established along dike shorelines, but made up less than 5% of total biomass (front cover—*upper photo*). By 1972, *L. salicaria* was approaching dominance in several areas of emergent-aquatic vegetation, especially where muskrats had foraged among cattail. At this time the senior author estimated that, overall, purple loosestrife made up roughly 30% of the biomass of emergent aquatic and dike-slope vegetation. We were not able to make observations in 1976, but 2 years later, during a brief visit to the study site, the senior author found that *L. salicaria* had not only dominated the cattail zone, it had spread upward into the dike slopes and outward into the floating aquatic zone and now made up more than 90% of the biomass of the vegetation (front cover—*lower photo*). The desirable mix of native food and cover plants had been displaced by *L. salicaria*. Figure 14 displays the establishment, expansion, and dominance of purple loosestrife as constructed from our biennial estimates of green biomass. Local establishment of seedlings probably

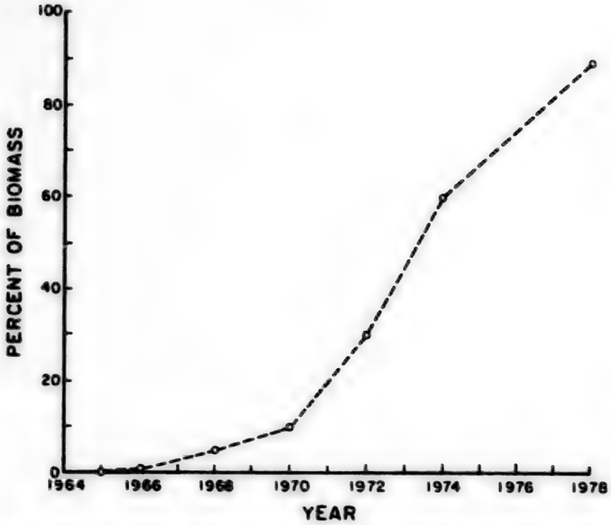

Fig. 14. Estimated percent of total biomass of dike cover made up by *Lythrum salicaria* from 1965 to 1978, green-tree reservoir, Montezuma National Wildlife Refuge.

occurred in the first year of flooding (1965); these scattered seedlings went unnoticed in 1965, but overwinter survivors gave rise to the solitary flowering stalks counted in 1966. A vast wetland complex adjacent to the experimental impoundment was infested with purple loosestrife and served as the water source for the green-timber impoundment units. This was doubtless the source of seeds and propagules pumped onto the experimental wetland at the beginning of each growing season. Furthermore, seeding was repetitive each year as pumping continued into the growing season to replace water lost to transpiration from the lush forest canopy. By the fifth year of operation (1970), purple loosestrife was widespread along the water control canals; it had increased to about one plant per 10 m^2 and made up about 10% of the biomass of dike vegetation. By this time, an accelerated phase of local expansion had begun that displaced more than half of the dike cover biomass within the next 4 years (1974). In another 4 years (1978), the rate of displacement slowed as the dike cover became a virtual monotype of purple loosestrife.

Haramis and Thompson (1984) emphasized the need for direct and secure routes to accommodate the post-drawdown movements of flightless juvenile wood ducks to marsh areas where they can complete their development. The Montezuma green-timber impoundment layout was weak in this respect; the dominance of purple loosestrife on sites that were designed as brood habitat greatly aggravated the problem. Several (two to five) pairs of Canada geese (*Branta canadensis*) nested on dikes or in flooded timber from 1965 to 1969. Broods from these nests were reared in low, open dike cover (mixed grasses and forbs) until 1969. By 1978, *L. salicaria* occupied about half of this foraging area. In addition to the loss of forage, goslings became more vulnerable to their principal predator, the red fox (*Vulpes vulpes*). Foxes now had enough concealment cover to make close approach to the goslings possible. The value of dike and berm cover for muskrats was also greatly reduced as their principal food (*Typha* spp.) was replaced by *L. salicaria*.

Although the infestation and dominance of the green-tree impoundment duck-brood cover was dramatic, it was not as sudden as that experienced following the drawdown of a shallow waterfowl display pool at the Sapsucker Woods Sanctuary near Ithaca, New York. Seedling densities (3–6/m^2) on exposed bottom sediments at Sapsucker Woods were similar to those at the Montezuma impoundments, but competition for space with existing native aquatic plants had denied purple loosestrife seedlings at Montezuma the opportunity to take over bare, exposed organic surfaces. The pool at Sapsucker Woods had been formed with shallow dikes that backed water into the edge of a relatively undisturbed hardwood forest. The pond bottom contour gently sloped toward the deeper waters of a waterfowl display pool. In 1955, wild-type purple loosestrife was planted on an open area on the deep side of the pond. Although the bottom contour of the pond was steep enough to prevent the spread of purple loosestrife into the pond, in the next 10 years it spread around the open edges of the pond and into openings in the forest canopy caused by the death of water-stressed trees. Meanwhile, a display-pool feeding program and accompanying high concentrations of migrant and resident waterfowl produced a heavy accumulation of spilled corn and waterfowl feces. The threat of botulism (D. Mills and M. Richmond, 1971–73, unpublished reports of New York Cooperative Wildlife Research Unit) made sediment removal an urgent necessity. Drawdown was begun on or about 20 July 1971; by early September (Fig. 15), the shallow flat in front of the forest edge had been colonized by a vigorous catch of 40-day-old *L. salicaria* seedlings. Delays with renovation problems extended the drawdown into October, by which time the young loosestrife seedlings were old enough to survive shallow flooding. Within 3 years following reflooding, the shallow pond zone was a solid stand of mature purple loosestrife.

Furbearers

The impact of the invasion of *L. salicaria* on North American muskrat and mink (*Mustela vison*) populations

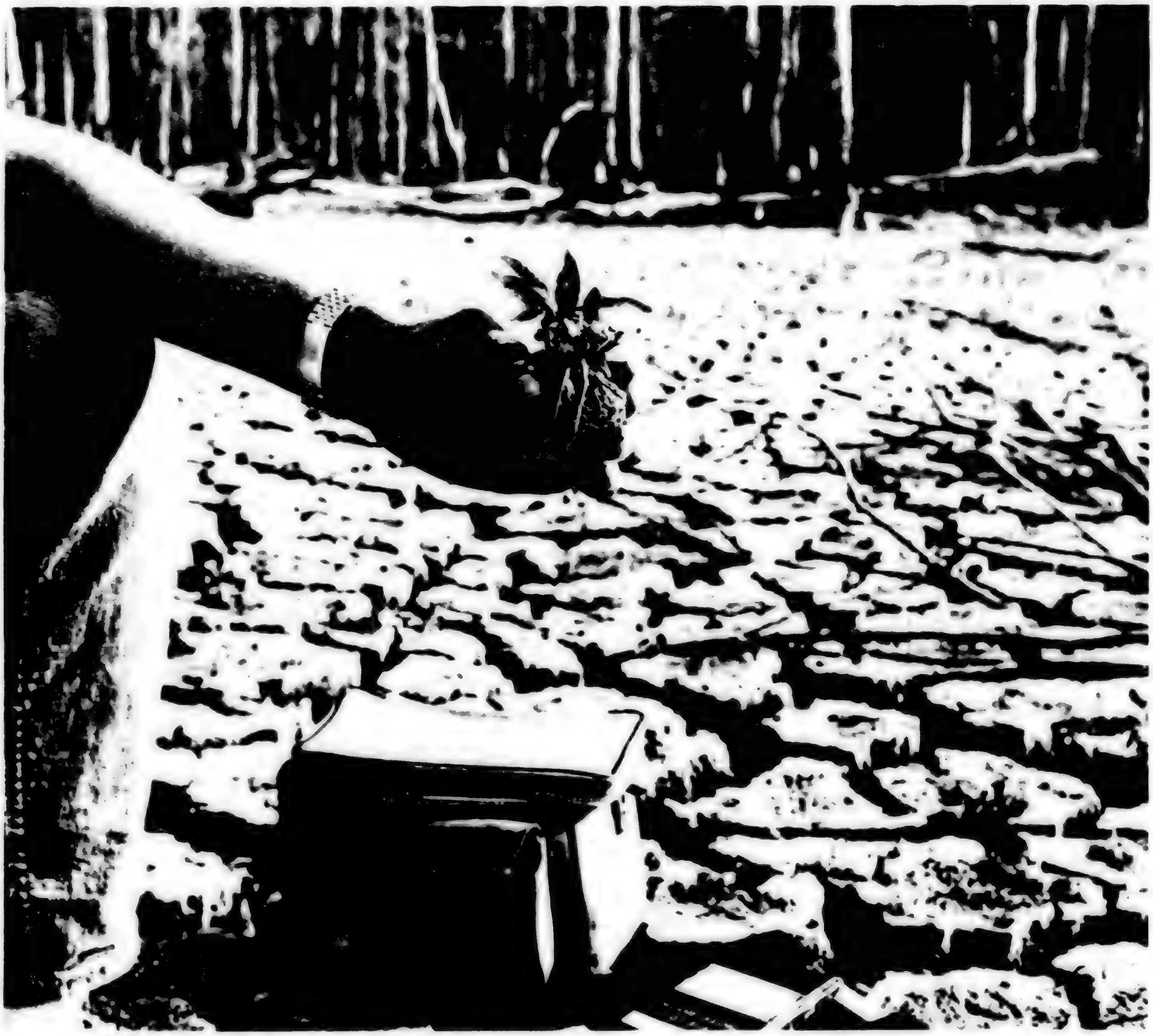

Fig. 15. Forty-day-old purple loosestrife seedling growing on bottom sediment exposed during renovation of waterbird display pool at Sapsucker Woods Sanctuary, Ithaca, New York, 19 September 1971.

has not been measured, but several interactions are probable. Muskrats themselves frequently hasten purple loosestrife dominance of local habitats through their selective foraging on its principal competitor, *Typha latifolia* (Fig. 16). In September of 1971, after a winter of muskrat abundance on the Montezuma NWR, the senior author observed muskrats foraging in an infested cattail stand. *Typha latifolia* stems in the vicinity of the active muskrat houses were heavily exploited, but *L. salicaria* stems were only partially cut. Many of the latter's stems were cut but not eaten; others were cut into short segments, partially gnawed into the periphery of the outer cortex, and discarded. Each of these partially eaten cuttings was a potential propagator of a new purple loosestrife plant. With rising water levels, many of these cuttings floated out into open water and were driven by wind and current against surface vegetation mats on adjacent shores. The removal of competing cattails, the rafting of cattail debris from muskrat foraging, and the spread of cut *L. salicaria* stems all suggested a favorable interaction for the dominance of the latter in an area that was largely deep-water cattail habitat. Furthermore, the shift from cattail to purple loosestrife foretold a permanent change in the carrying capacity of the habitat for muskrats and

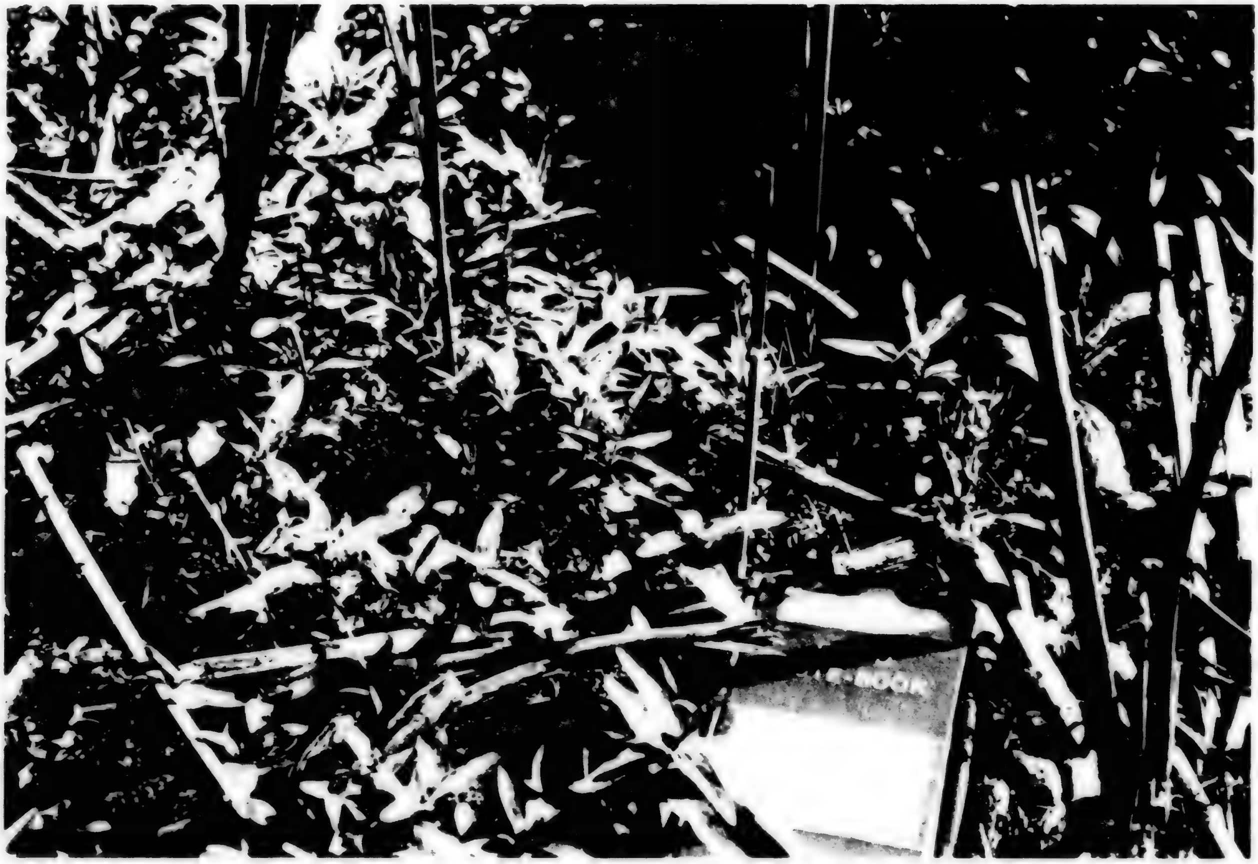

Fig. 16. Muskrat foraging in broad-leaved cattail has favored the establishment and survival of *Lythrum salicaria* seedlings. Montezuma National Wildlife Refuge, 30 September 1971

waterbirds. With decreasing prey species, a decline in mink numbers was another probable outcome.

Impact on Declining Species

Purple loosestrife's ability to usurp wetland habitats is worrisome in view of the vulnerability of threatened native wetland plants and wildlife. Fernald (1940) toured the St. Lawrence flood plain below Montreal and reported that ". . . the formerly unique and endemic flora of the estuary is being rapidly obliterated by . . . flowering rush (*Butomus umbellatus*) and the purple loosestrife (*Lythrum salicaria*) both . . . without mercy for the insignificant endemics. . . ." More recently, Coddington and Field (1978) suggested that crowding by *L. salicaria* may be partly responsible for the decline of a threatened bulrush (*Scirpus longii*) in Massachusetts. Rawinski (1982) observed that a rare inland population of dwarf spike rush (*Eleocharis parvula*) in inland New York seemed immediately threatened by invading purple loosestrife. Among vertebrates, several species deserve special attention.

Bog Turtle

The bog turtle (*Clemmys muhlenbergi*) is a small, uncommon, and poorly known reptile that is restricted to wetlands and bogs in the eastern United States (Bury 1979). The northern portions of its range have long been colonized by *L. salicaria*. Shallow, standing water and wet, open fen or meadow with muck substrate are favored habitats for the bog turtle. These are also sites that are readily invaded by purple loosestrife, particularly following disturbance to the habitat from grazing or drainage. The domination of these sites by tall, dense monospecific stands of *L. salicaria* causes a dramatic change in the physical as well as the trophic structure of the habitat (Kiviat 1978) and further aggravates the tenuous status of the bog turtle in the northern segments of its range.

Black Tern

The continuing invasion of purple loosestrife into glacial basins in the north-central States comes at a difficult time for the black tern (*Chlidonias niger*). These graceful birds have always been an abundant breeding species in the shallow ponds throughout the northern prairies and Great Plains (Bent 1921). Faanes (1979) recently reported an alarming decline of the black tern in Wisconsin. In addition to the habitat shrinkage described by Faanes (1979), the invasion of shallow pond borders by *L. salicaria* will probably render typical black tern nest sites unusable. Terns prefer open surface litter, such as the top of an abandoned muskrat house, as nest sites. These would also be likely places for purple loosestrife seeds, propagules, or muskrat cuttings to lodge and take root. Once the species becomes established, the open character of the black tern nest platforms is lost.

Canvasback

The canvasback (*Aythya valisineria*) has never recovered from the low levels of the great "duck depression" brought on by the disastrous drought of the early 1930's. The species has been nearly simultaneously beset with loss of nesting habitat in the prairie pothole region (Fig. 8) and a gradual decline in the quality of its restricted wintering grounds (Trauger 1974). Its preference for platform nests built over water in cattail, *Typha latifolia*, or hard-stem bulrush, *Scirpus acutus* (Stoudt 1982) makes it vulnerable to encroachment by purple loosestrife. Fortunately, *L. salicaria* seems to be slow in colonizing the prairie pothole region. A plant was collected at Neepawa in 1896 (Stuckey 1980), but the species did not begin to spread into Manitoba wetlands until after 1950. It may prove to be less vigorous than native plants in competing for space under the harsh and widely fluctuating climatic patterns of the northern prairies. The relative isolation of prairie pothole sloughs also makes spread by waterborne propagules a slow process. Nevertheless, it invaded Delta Marsh in 1955 and has required vigorous local control in disturbed areas along the marsh edge (H. Hochbaum, personal communication; Friesen 1966). With drawdown or drought, *L. salicaria* could threaten the deep-water nesting areas of the canvasback at Delta.

Western Riparian Habitat

A recent report (Brezenski, personal communication, 31 August 1981) of an infestation on the Platte River floodplain near Elm Creek, Nebraska, indicates that purple loosestrife may become troublesome in Great Plains streams. Brezenski discovered fully developed stands around the margins of several ponds in the Blue Hole Wildlife Area. Two-thirds of the shoreline of the largest pond (Blue Hole) was bordered by a tall and vigorous stand of purple loosestrife that had completely displaced all other cover (Fig. 17).

All of the ponds in the Blue Hole area were constructed as mitigation units to replace riparian habitat destroyed by the construction of Interstate Highway 80. The pond substrates and margins were alluvial sand. Water quality of seepages supplying the ponds was excellent. Fishing was also attractive and bank fishermen trampled purple loosestrife stalks along the shoreline to make room for their sport. Unfortunately, the stalks that were trampled outward into the pond developed aerenchyma along the submerged stems, and sprouted adventitious root and stem buds. By these means, the species had moved outward over a shallowly (1:8) sloping bottom. Unusually high and prolonged flooding in the spring and early summer of 1983 scoured the shorelines of Blue Hole and greatly reduced purple loosestrife abundance; however, by the end of the 1985 growing season, *L. salicaria* was obviously a hardy and aggressive survivor. It had spread along the scoured outlet of Blue Hole and colonized new habitats on each side of the stream. It had also colonized an adjacent pond where it was displacing a native flatsedge (*Cyperus erythrorhizos*) along the pond margin (D. Q. Thompson, unpublished field notes).

Although it is too early to assess the impact of the Blue Hole infestation, the potential for habitat degradation is very serious. An ecological study of sandhill cranes (*Grus canadensis*) along the Platte and North Platte rivers (USFWS 1981) showed that about 80% of North American sandhill cranes use this area as a migratory rest stop enroute to their boreal and subarctic breeding grounds. Flood control and irrigation structures in Colorado, Wyoming, and western Nebraska divert about 70% of the Platte's annual waterflow, resulting in reduced scouring of sandbars and less shifting of alluvial sediments. Thousands of hectares that were formerly emergent aquatic vegetation are now overgrown with woody vegetation and unattractive to sandhill cranes (USFWS 1981). Krapu et al. (1984) estimated that about 0.5 million cranes use shallows and sandbars along 111 km of open river channel as night roosts. By using the estimates of Krapu et al. (1984) we calculated that about 0.4 million of these cranes use night roost sites downstream from the Blue Hole infestation. Management plans for the crane staging areas recognize the need to keep existing roosting sites open and to bring over-

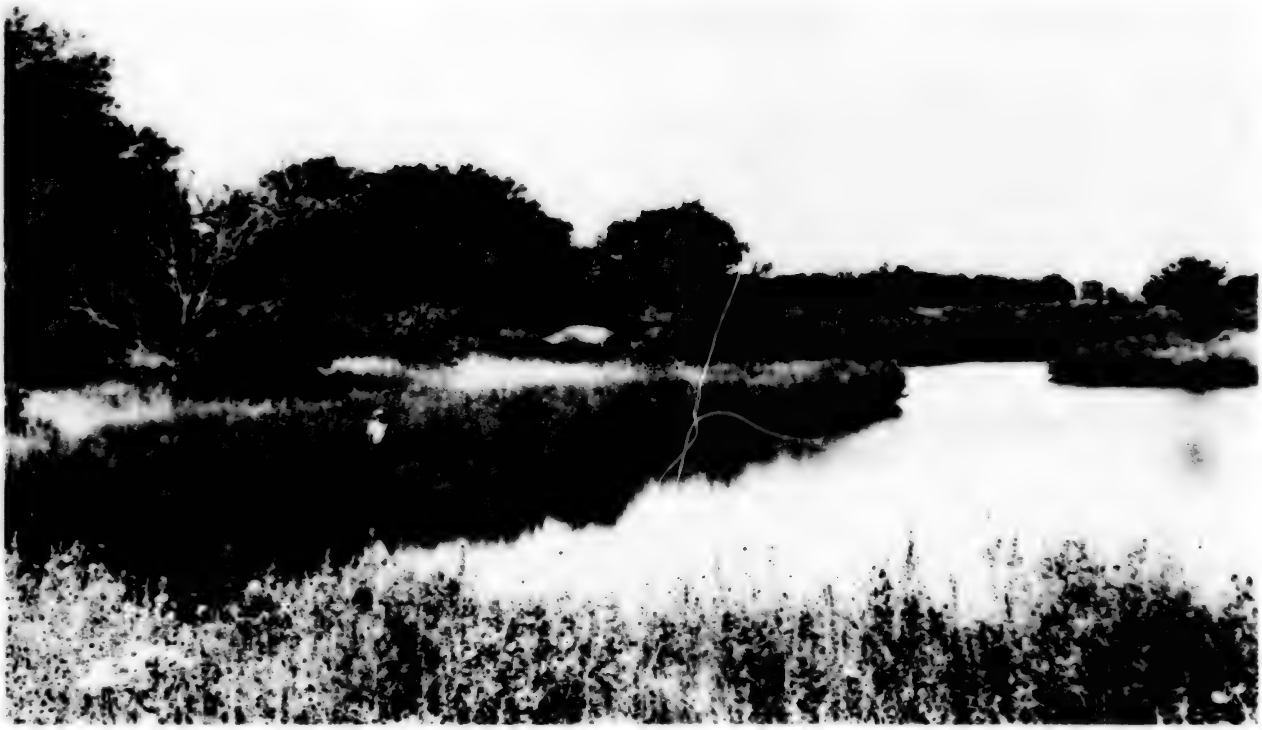

Fig. 17. Purple loosestrife infestation around the south rim of Blue Hole—a mitigation pond in sandhill crane Staging Area 2 near Elm Creek, Nebraska, 4 September 1981.

grown areas back to earlier seral states. The presence of purple loosestrife in many of these sites seriously complicates these management plans.

Other reports of *L. salicaria* in Nebraskan riparian habitats come from the Niobrara River along the north-central border. In 1980, the plant was collected at two sites by botanists from the University of Nebraska–Lincoln (R. B. Kaul, letter, 15 February 1982). More recently, K. Menzel (letter, 14 August 1984) reported that *L. salicaria* infestations are now more or less continuous along 20 km of the Niobrara from south of Norden to Meadville, with another concentration near the bridge north of Newport.

A last example of the successful colonization of a western riparian site comes from Wyoming. The first and, to our knowledge, only report of purple loosestrife from this State is from a field collection made by State botanists in 1979 (Lichvar and Dorn 1980). Visits to this site by the senior author in 1982 and 1983 showed a mature stand of purple loosestrife that had invaded about 1 ha of wetland. This slough had developed in a former dry wash that had become a permanent wetland with the establishment of the Shoshone Reclamation Project in the 1930's. About 30 cm of sediment and organic debris had accumulated in 50 years of seepage and runoff. Despite vigorous stands of *Typha latifolia*, *Scirpus acutus*, and *Carex* spp., *L. salicaria* had spread throughout the small slough and threatened to dominate the site (Fig. 11).

Impact on Agriculture

Purple loosestrife is not a likely threat to cultivated crops. The large perennial rootstocks of *L. salicaria* lie within the upper 30 cm of the soil profile and are thereby susceptible to any form of crop culture that includes annual tillage. Moreover, because purple loosestrife seed is primarily distributed by flowing water, upland crops are secure from infestation even in the presence of lowlands heavily infested with the species. The establishment of *L. salicaria* adjacent to wild rice (*Zizania aquatica*)-growing areas of northern California (D. Barbe, personal communication) opens the possibility of the infestation of wild rice stands. In an earlier report from this region, Howell and True (1966) stated, "Dr. T. C. Fuller tells us that the plant has become so rampant at the last station [roadside ditch, 2.5 miles south of Oroville, Butte

Co.] as to require agricultural control since it threatens to invade rice fields." We have also received a report from Wisconsin (unpublished Purple Loosestrife Task Force Newsletter, October 1986) of concern that wild rice beds on the Lac du Flambeau Indian Reservation might be threatened by *L. salicaria*.

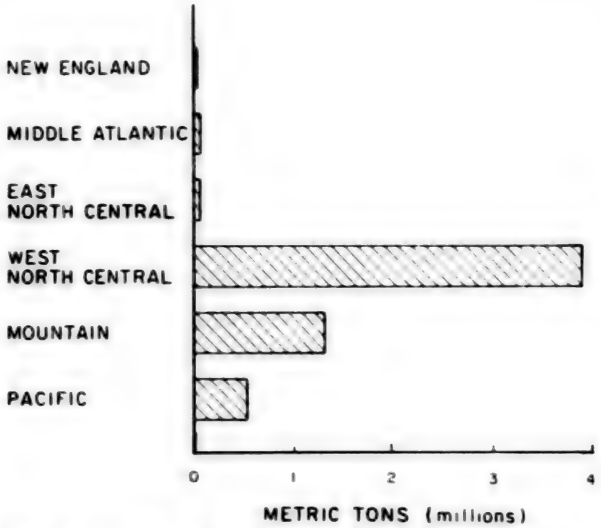

Fig. 18. Millions of metric tons (dry weight) of wild hay harvested in 1974 in six regions of the northern United States (USBC 1977*b*).

Wetland Pasture

Although Fernald (1940) and Muenscher (1955) recognized the threat that *L. salicaria* posed to native wetland plants, the first report of this plant as an agricultural weed came from the pastures along the floodplain of the St. Lawrence River between Montreal and Quebec (Louis-Marie 1944). In 1942, Quebec's Ministry of Agriculture requested Louis-Marie to begin a study of the growing complaints of farmers and villagers, particularly in the region of Lac St.-Pierre, where it "usurps pasturage from more than 800 cows." After two seasons of field work, Louis-Marie estimated that the infestation covered 5 square miles. He also reported that the livestock forage value of lower meadows, where *L. salicaria* had established monospecies stands, was negligible. This difference in palatability between *L. salicaria* and native forages (grasses and sedges) is one of the keys to purple loosestrife's success as a pasture invader. The early foliage of *L. salicaria* is palatable to livestock (also to white-tailed deer, *Odocoileus virginianus*); the mature plant is much less frequently taken and therefore has a growth advantage over its heavily clipped associates. The wetland pastures that typically occur along floodplains and on the peripheries of glacial marshes throughout New York, Wisconsin, northern Iowa, and southern Minnesota are highly vulnerable to *L. salicaria* invasion.

Wild Hay Meadow

The cutting of wild hay has been in slow decline over the past 50 years; however, the number of hectares harvested changed very little from 1969 to 1974, and has remained well above 2,832,900 ha (7 million acres) over the United States (U.S. Bureau of the Census [USBC] 1977*b*). Figure 18 displays the millions of metric tons of wild hay harvested in six regions of the northern United States in 1974. Several aspects of these statistics need to be considered before evaluating the possible impact of *L. salicaria* on wetland or riparian hay marshes. First, in Fig. 18, wild hay is excluded from those States in which purple loosestrife does not occur or is not a threat. Second, the wild hay statistic does not separate wetland and riparian hay meadows from upland sites that would not be susceptible to *L. salicaria* invasion. From our field observations, we judge that lowland meadows make up more than half of the totals shown. Third, the degree that purple loosestrife will be able to invade wild hay marsh is difficult to estimate. In the absence of selective grazing pressure that occurs in meadows used for pasture, wild hay fields that are mowed annually will be more resistant to invasion by alien species. That *L. salicaria* will indeed invade wild hay meadows has already been demonstrated at sites in the Northeast, Midwest, West, and Pacific Northwest. At each of these sites, purple loosestrife has invaded ungrazed stands of grass or sedge. Last, the most useful concept to be drawn from Fig. 18 is that the potential damage to wild hay is inverse to the present distribution of purple loosestrife infestations. Wild hay cutting has been in decline in the Midwest and Northeast where it had a wide variety of uses including dunnage for ship cargos, fiber for carpets, and forage and bedding for livestock. With the coming of improved upland forage crops, wild hay fields in these middle and eastern areas have reverted to marginal pasture, with many thousands of hectares passing out of agricultural usage. The picture is very different in the western ranges that have traditionally produced most of our feeder cattle. The quantity and quality of the western wild hay harvest determine the growth and survival of overwintering yearlings and the health and success of the spring calf crop. The largest blocks of wild hay in the United States lie in western riparian meadows; the next 10 to 20 years will determine the impact of *L. salicaria* on this forage resource.

History of Control Efforts

We could find no descriptions of *L. salicaria* control efforts in Europe. Nevertheless, Morse and Palmer (1925) listed purple loosestrife as a semiaquatic weed in Great Britain and recommended the following control procedures for this group of weeds: "Weeds along the margins of ditches and watercourses should be cut regularly, and ditches thoroughly cleared in the autumn." Similarly, Woodford and Evans (1965) listed *L. salicaria* as an emergent weed along British waterways.

Quebec

The pioneer work of Louis-Marie (1944) mentioned earlier in this paper was the first report of the control of purple loosestrife in North America. Following a year of preliminary study during 1942, Louis-Marie established an elaborate set of 32 field plots in the floodplain pastures north and east of Pierreville, Quebec, on the south shore of Lac St.-Pierre. In the summer of 1943, he applied mowing, crushing, hand-pulling, flame torch, and chemical treatment to these plot groups. Unfortunately, his efforts were interrupted after the end of the 1943 field season, leaving the critical question (frankly recognized by Louis-Marie) of rootstock recovery in the next growing season a suspended judgment. Nevertheless, his first-year results indicated that repeated mowing would be one of the most effective means of reducing *L. salicaria* infestations in pastures. His application of fire did not include the usual tactic of igniting dead surface litter in fall or spring. Rather, green plants were hit directly with a flame torch during the growing season. Louis-Marie thought that the flame torch results were parallel to the effects of mowing, but more costly to apply. Similarly, his attempts with crushing and hand-pulling were thought not to be cost effective on large areas. Sodium chloride and chlorate were the chemicals tested; although *L. salicaria* was more susceptible to desiccation than grasses or sedges, the differences in mortality were not great enough to recommend further efforts.

In addition to his experimental work, Louis-Marie recommended some control methods that were based on the experiences of local farmers and his own field observations. Noting that the most dense stands of purple loosestrife were in areas of soil that were saturated by annual flooding, Louis-Marie recommended that a drainage system be constructed to reduce the vigor of what he referred to as "a vast *Salicaria* colony of five square miles." He also recommended a schedule of repeated mowing in concert with continuous grazing pressure to reduce the vigor of the colony. In areas of heaviest infestation, he suggested that deep discing followed by harrowing be used to kill rootstocks. Louis-Marie recognized that rootstocks upended by the harrow might make the work of mowing very difficult. The only subsequent mention that we can find of the Lac St.-Pierre area was from Gagnon (1953), who reported that despite many years of control efforts, purple loosestrife was still a serious pasture weed at Lac St.-Pierre.

Although the control methods employed by Louis-Marie were acceptable for agricultural land (drainage, discing, repeated mowing), they would not be compatible with the maintenance of natural areas or with most wildlife habitat objectives, where the need to maintain community integrity recommends minimum impact methods. It is nonetheless unfortunate that Louis-Marie was not able to continue his work. With the possible exception of Rawinski's work (1982), no one has attempted such an ambitious field study of *L. salicaria* in North America.

New York

Lower Hudson

By 1960, more than 1,000 small impoundments had been created in New York State to provide new wetland habitat, particularly for waterfowl (Emerson 1961). Unfortunately, by this time *L. salicaria* was so widely distributed in the uplands of the lower Hudson district that McKeon (1959) reported "a large percentage of marshes in the district have an almost pure stand of purple loosestrife (*Lythrum salicaria*) which provides little food but does give some cover." McKeon chose a 4.9-ha (12-acre) marsh constructed in 1952 as the site of *L. salicaria* control studies. By 1955, the central portion of this marsh had become "almost completely dominated by purple loosestrife with a few sedges interspersed." Water level manipulation, burning (in winter), and cutting at surface and subsurface were attempted in sequence, with no success. Six different commercial herbicides (Weedazol, 2,4-D, 2,4,5-T, Karmex 40, 2-4 Dow, and Kuron) were sprayed on trial plots from 1955 to 1958. Although 100% top kill was obtained with three of the sprays, regeneration from rootstocks frustrated control attempts. McKeon concluded that none of the herbicides would be cost effective in management operations. Reports from this district in 1980 (G. Cole, personal communication) indicated that purple loosestrife continued to be a serious problem in the lower Hudson wetlands.

Upstate

Although *L. salicaria* was not a problem in the uplands of central New York in the early 1950's, it had been long established along the New York State Barge Canal (Dudley 1886; Wiegand and Eames 1926) and had become troublesome in two wetland management areas bordering the canal. L. S. Smith (1959) reported on problems with purple loosestrife encroachment into impoundments of the Montezuma NWR following maximum drawdown in 1954 and 1955 to achieve carp (*Cyprinus carpio*) control; he used a truck-mounted sprayer to apply ammonium sulfamate to stands along impoundment shorelines. This resulted in a complete kill of plants within reach of the spray rig; nevertheless, plants in the pool interior could not be reached and the infestation continued to increase on the refuge. Smith considered purple loosestrife to be a serious threat to impoundment manipulation. Meanwhile, in nearby Howland Island Game Management Area, R. H. Smith (1964) began work on loosestrife control in a set of shallow waterfowl impoundments that dropped from a full head of 60 cm in spring to nearly dry soil in August. He was able to obtain partial control with silvex (2[2,4,5-trichlorophenoxy] propionic acid) and mixtures of 2,4-D (2,4-dichlorophenoxyacetic acid)and 2,4,5-T (2,4,5-trichlorophenoxyacetic acid); however, he found it necessary to repeat spraying in subsequent seasons to control resprouting and seedling growth. Smith (1964) concluded that if water levels in shallow impoundments were to be manipulated in the presence of purple loosestrife, spraying of mature plants and seedlings would need to be carried out during drawdown and repeated following reflooding.

Other Problem Areas

Similar problems with *L. salicaria* in shallow impoundments have been reported from Massachusetts (G. Gavutis, Parker River NWR, unpublished report) and Ohio (R. Kroll, Sandusky Bay, personal communication). Purple loosestrife also escaped into Delta Marsh (H. A. Hochbaum, personal communication; Friesen 1966) where it was difficult to control. More recently, reports have come from the Ada County Weed Control Office at Meridian, Idaho, that *L. salicaria* invaded a wet pasture bordering the Boise River in 1972 (W. E. Hartman, personal communication).

Common Pattern

A common pattern can be seen in these early experiences with the control of purple loosestrife in marsh basins in eastern and midwestern North America. First, a long lapse of time has occurred (50 years or more) between the earliest records of local occurrence and the recognition that a serious infestation had become established. This may suggest a period of acclimation and the selection of ecotypes, or it may simply be a reflection of the relatively slow spread of the plant from local seed sources. Second, all of the serious infestations occurred under conditions that suggest that waterborne seeds or propagules were responsible for dominance of *L. salicaria* in the local habitat. Third, all of the habitats dominated by loosestrife were occupied by native vegetation that was growing under stressed or disturbed conditions. Drainage of deep-water basins, flooding of shallow basins, or seasonal drawdowns of impoundment pools were all characteristic of the areas of heavy infestation in northeastern North America. Last, once the local infestation was established, all available control measures were inadequate in providing control with a reasonable expenditure of funds and effort.

Recent Control Efforts

Chemical

Until the 1980's, the resistance of purple loosestrife to available herbicides gave wetland managers a limited list of compounds for controlling this hardy exotic. Although not approved for aquatic use, dicamba (Banvel: 3,6-dichloro-o-anisic acid) was used on experimental plots at Parker River NWR with modest success (Parker River NWR, 1972 unpublished field report). A mixture containing equal amounts of dicamba and 2,4-D was applied to the infestation near Meridian, Idaho. Reed canarygrass was the dominant forage at this site; the infested area was accessible to power spraying equipment. Despite treatments during early bloom in 2 successive years, a scattering of surviving purple loosestrife plants in August of 1980 (D. Q. Thompson, unpublished field notes) indicated that the site was still threatened with a resurgence of the infestation. Our earlier reference to the work of Gilbert and Lee (1980) suggests that summer dormancy of a small percentage of *L. salicaria* root crowns could account for some of the difficulty of controlling this weed with chemicals.

Prospects for chemical control changed sharply with the advent of glyphosate (Roundup: *N*-[phosphonomethyl] glycine). First described by Baird et al. (1971) as a postemergence spray for the control of perennial herbaceous weeds, this broad-spectrum herbicide has many attributes that support its use on agricultural lands. It is a systemic compound that is absorbed by leaf surfaces and translocated to the entire plant, including roots and underground stems. It is effective at relatively low concentrations and has a low potential for bioaccumulation. The half-life of its biological activity in soil and water is fairly short—about 2 months (Rueppel et al. 1977). It is of relatively low toxicity to birds (Batt et al. 1980), mammals (Monsanto, mimeo. report), and aquatic invertebrates and fish (Folmar et al. 1979). The effectiveness of glyphosate in agriculture soon led to applications on perennial weeds on rangeland (Gottrup et al. 1976), ornamentals and Christmas tree plantings (Ahrens 1974), and in general forestry (Sutton 1978). The first report of use in an aquatic habitat is from Welker and Riemer (1982), who used glyphosate to control an infestation of fragrant waterlily (*Nymphaea odorata*) in New Jersey with application rates of 2 and 4 pounds per acre in successive growing seasons. The second year, spraying was needed to control seedlings germinating from seeds in bottom sediment and resulted in eradication for at least 3 more years. Rawinski (1982) and Malecki and Rawinski (1985) reported on *L. salicaria* tests at the Montezuma NWR in central New York; they used replicated plots to test three rates of glyphosate application (1.7, 3.4, and 6.7 kg/ha) against three stages of growth (vegetative, 13 June; early flowering, 13 July; late flowering, 11 August). Results showed no significant difference in application rates but a highly significant difference in the timing of applications. The late flowering application was the most effective with nearly 100% shoot reduction. In the following growing season, Rawinski found that the timing of application also affected the establishment of purple loosestrife seedlings—the plots sprayed in June became reinfested with seedlings, whereas the plots sprayed in July and August were free of purple loosestrife seedlings. Furthermore, the infested plots were colonized by several species of desirable waterfowl food plants. Despite the promise of these results, Rawinski (1982) cautioned against the widespread use of glyphosate without adequate knowledge of the effects of this new chemical on marsh ecosystems.

Christy et al. (1981) studied the effects of glyphosate on the growth rate of *Chlorella sorokiniana*. They reported the glyphosate concentration threshold for zero growth to lie between 17.7 and 23.7×10^{-6} M. In limited tests, they also found supporting evidence for soil inactivation of glyphosate with Kaolinite. They concluded with a warning (similar to that of Rawinski) that careless use of glyphosate in aquatic systems "could result in elimination of beneficial species, proliferation of noxious species, and disruption of food chains and/or nutrient cycles." The criticism of use of chemical controls on natural habitats hinges on the percentage of habitat treated and the care with which the treatment is delivered. The delivery system should be as gentle and as target specific as possible.

In 1982, a new formulation of glyphosate (Rodeo-EPA Reg. No. 524-343) was approved for use over water (J. B. Elder, USFWS memo, 14 February 1983). The new formulation includes the same active ingredient (glyphosate), but uses a new surfactant (Ortho X-77). Several field tests with the new formulation have shown that glyphosate is very effective in reducing large monotypes of reed (*Phragmites australis*) in eastern wetlands (G. W. Gavutis, USFWS memo). Similar work was conducted on purple loosestrife in marshes in northeastern Ohio (Balogh 1986).

Cultural

Water Manipulation

The response of various growth stages of purple loosestrife to water levels is not well known. Without specifying water depths or timing, McKeon (1959) reported that water manipulation attempts on Travers Marsh (5 ha) were "completely unsuccessful." However, G. Cole (personal communication) reported that raising the water level about 60 cm in the 1960's resulted in the retreat of a monotype of purple loosestrife to the rim of this marsh leaving the deeper (120–150 cm) portions of the impoundment free of the plants. R. H. Smith (1964), doubtless referring to mature plants, stated that purple loosestrife will "survive for many years even when submerged to depths of 2 or 3 feet. . . ."He did not attempt to use higher impoundment levels to control loosestrife and, indeed, could not raise the water on his experimental plots to more than 60 cm depth. Rawinski (1982) did not attempt to use flooding as an experimental procedure, but several of his field studies offered insights into the relation of water levels to purple loosestrife vigor and abundance. One set of plots compared the number of loosestrife and cattail shoots in a nearly monospecific stand of *L. salicaria* with an adjacent mixed-species stand (55% loosestrife: 44% cattail). Water levels were maintained at 40 cm depth throughout 3 years of study (1978, 1979, 1980); during this time the densities of loosestrife shoots decreased sharply in both sets of plots, whereas cattail increased threefold in the loosestrife plots and decreased to about two-thirds of its original densities in the mixed-species plots. Rawinski attributed the decline in loosestrife as "probably due to the combined effects of high water levels, damage by carp, and suppression by cattail." The effect of autotoxic feedback on *Typha latifolia* (McNaughton 1968) was not mentioned by Rawinski—but may have been responsible for some of the decrease observed in cattail shoots in the mixed-species stands.

Replacement Control

The use of replacement control in native wetland communities has limited value in that the cure (discing and seeding) is potentially as disastrous to the infested community as the invading weeds. In some circumstances, however, this may be the habitat manager's best choice. To control purple loosestrife in badly infested agricultural fields, Muenscher (1955) recommended plowing and planting an intertilled crop. Novak (USFWS Field report, Region 5, 1967) described the control of a heavy purple loosestrife infestation at Great Meadows NWR near Concord, Massachusetts; the field was mowed repeatedly, plowed, and planted to reed canarygrass. Rawinski (1982) tested seven plant replacements for purple loosestrife and found that Japanese millet (*Echinochloa frumentacea*) and reed canarygrass were promising, in the order mentioned. Thereafter, a large-scale field trial was conducted to test the ability of Japanese millet to suppress naturally occurring loosestrife seedlings resulting from an early July drawdown. The millet seeding was especially successful on deep-muck sites. In addition to suppressing loosestrife seedlings, the mature emergent millet stands were used by mallards and black ducks (*Anas rubripes*). This was a minimum disturbance replacement in that Rawinski used a hand-cranked machine to seed the newly exposed bottom. Furthermore, Rawinski indicated that Japanese millet is not likely to become a weedy intruder where used in natural habitats.

When summer drawdown of infested wetlands cannot be avoided, seeding exposed muck flats with Japanese millet is a good temporary measure to forestall the establishment of purple loosestrife seedlings. This would be particularly useful on, say, an intensively used waterfowl display pool where the exposed flats were accessible for hand seeding. It would be less useful on large impoundments with scattered emergent stands and many remote flats.

Fire

The growth form and phenology of purple loosestrife indicate that it will probably not be susceptible to control with fire. As an herbaceous perennial, its overwintering growing points on the crown of the rootstock lie about 2 cm below the soil surface, where they are fairly well insulated from the heat of a surface fire. Furthermore, *L. salicaria* begins spring growth about a week or 10 days after broad-leaved cattail and reed canarygrass, thereby reducing the chances that a spring burn would decrease the vigor of the weed. Also, fuel energy tends to remain concentrated in the erect overwintering stems rather than accumulating as fine-textured fuels at the soil surface. This shortcoming was demonstrated by an unsuccessful prescribed burn on a 1.6 km-long dike at the Montezuma NWR in the spring of 1971 (D. Q. Thompson, unpublished field notes). The dike cover had been seriously overgrazed by Canada geese in preceding growing seasons, leaving a patchy distribution of mixed grasses and forbs that had been invaded by small, scattered clumps of purple loosestrife. Although a slow, backing fire would have caused maximum heat penetration to the loosestrife root crowns, the distribution of surface fuels lacked enough continuity to maintain a moving line of fire. We were forced to use a head fire, with many patches needing separate ignition to finish the task. In the following year, mortality to loosestrife root crowns was less than 10%; the remaining crowns made vigorous growth and new seedlings continued to expand the dominance of the weed in the dike cover.

The Case for Biological Control

Concept

DeBach (1964) identified the field of biological control as comprising the "study, importation, augmentation, and conservation of beneficial organisms for the regulation of population densities of other organisms. . . . Particular emphasis has been laid on pest insects and mites, and weeds." The concept of classical biological control arose from the observation that some of the most damaging plant or insect pests in North America were aliens that were native to the Eurasian Continent and were spread worldwide with the rise of marine exploration and commerce. Moreover, the arrival of a potential pest species as a seed or egg enabled it to escape diseases, parasites, and predators that had coevolved with it. The assumption was made that these organisms, singly or in combination, limited the competitive vigor of the plant on its continent or area of origin. The application of this concept to the classical biological control of weeds was to search the native range of the weed for organisms (insects were the most obvious predators) that could be safely transplanted into the weed's new range. The goal of biological control was not the extirpation of the alien, but rather its reduction to a level that was acceptable. The trick was to find a natural enemy that was highly host specific, but could still survive when its target had been reduced to acceptable densities. This would produce the most cost-effective result, that is, the pest species and its control agent would oscillate within acceptable limits without further expenditure of control effort.

Although early critics of biological control of weeds (Forbes 1880; Thompson 1930) implied that it is a risky and unproven enterprise, its beginnings reach back to 1863 when an introduced cochineal insect (*Dactylopius ceylonicus*) was used to control naturalized cactus (*Opuntia vulgaris*) in southern India (Goeden 1978). In comparison, Batra (1982*b*) noted that the early use of toxic substances (salt, oil, plant extracts, lime, and soot) continued until the mid-1800's when simple herbicides (sulfuric acid, iron sulphate, copper sulphate, arsenic, sodium chlorate, and others) came into general use.

Taylor (1955) doubted that biological control of weeds would produce enough successful results to warrant serious consideration as an alternative to chemical control. Huffaker (1959) countered these and other detractors of the soundness of the concept by asserting that "Textbooks on plant ecology . . . ignore the role phytophagous insects may have on the composition of vegetation. This omission results from their emphasis on the plant environment and the climatic and edaphic factors, with a consequent neglect of biotic forces . . . ." Wilson's (1964) apprehensions that "the main limiting factor in the application of biological control to weeds lies . . . in the risk that useful plants will also be attacked" have been tempered by a later assessment (Wilson 1974) that "many important successes and exciting developments" had been achieved, including "control of winter moth (*Operophthera brumata*) in Canada, and of Crofton weed (*Eupatorium adenophorum*) in Hawaii and elsewhere . . . ." To these successes, one could add the control of alligatorweed (*Alternanthera philoxeroides*) in southeastern United States with insects (Maddox et al. 1971; Brown and Spencer 1973; Spencer and Coulson 1976), successful control of an alien plant (*Salvinia molesta*) in subtropical Australia by an imported weevil, *Cyrtobagous singularis* (Room et al. 1981), and promising results with the suppression of water hyacinth (*Eichhornia crassipes*) in Louisiana by an imported weevil, *Neochetina eichhorniae* (Goyer and Stark 1981).

During the past 80 years, a pattern of investigation has been constructed to guide the work of applied biological control. These procedures have become known as "Classical Biological Control" and were listed by Batra (1982*a*) in the following sequence.

1. Weed candidate for biological control is studied to determine its probable origin, potential to cause economic damage, existing natural enemies, and beneficial uses or values.
2. This information and basic ecological data on the pest species is reviewed by an interagency panel of scientists representing about 10 disciplines or responsibilities; Canadian and Mexican comment is also sought if control organisms are likely to disperse across an international boundary.
3. After approval by the interagency panel, search and study are begun of the weed's natural enemies in or near the center of its native range.
4. Ecological studies are done of the most damaging and host specific natural enemies.
5. Exhaustive screening tests are made with the candidate control agents. Host specificity tests are made with crop, horticultural, and native plants related to the weed. If the candidate attacks only its weed target, it is subjected to starvation tests in the presence of possible alternative hosts. If it does not survive in the absence of its target, it is considered safe for trial in the United States.
6. A report on the candidate agent is reviewed by interagency scientists; Federal and State quarantine permits for importation and release of the agent are obtained.
7. The agent is screened in quarantine to eliminate its own parasites.
8. The agent is released in field cages to observe behavior, survival, and reproduction in the habitat of the target species.
9. The agent is released in undisturbed habitats that contain extensive infestations of the target weed.
10. From these foci, the agent multiplies and spreads into adjoining infestations. Cooperators throughout the target weed's range can hasten the spread of the control agent by redistributing local materials.

An additional step should be added, namely, an evaluation of the efficacy of the introduced agents, including their impact on native biota—particularly plants that are closely related to the target weed. Klingman and Coulson (1982) prepared a detailed set of guidelines for the introductions of foreign organisms as biological control agents. Their paper codifies all procedures and identifies the missions of various Federal facilities.

The deliberate and complex nature of a biological control program requires 10 or more years before results are obtained in the field; however, cautious and time-consuming testing procedures have borne exemplary results. Batra (1982*b*) pointed to more than 100 host-specific phytophagous insect species introduced worldwide without serious losses arising from introduced agents attacking beneficial plants.

The objectives and methods of biological control are ideally suited to coping with purple loosestrife's invasion of North American marshes and riparian wetlands. The high degree of host specificity demanded by testing and field trials makes biological control extremely compatible with the wildlife or natural area manager's goal of maintaining community integrity and ecological health. In addition to having a specific target, biological control is relatively gentle—it eschews extermination and aims instead at reducing the pest species density to some acceptable minimum.

Criteria of a Biological Control Target

Several criteria are useful for evaluating the need for a biological control program. First, the introduced weed must have clearly demonstrated a potential for doing serious damage over a large area. Second, alternative means of effective control must have been tried and found to be inadequate or infeasible. Third, no economically or ecologically useful plants should be near relatives of the target species. We think that our previous discussions of the spread, impact, and control of purple loosestrife have met the first two criteria. Of the third criterion, *L. salicaria* has no near relatives of economic value. Among more than 20 genera and 400 species of Lythraceae throughout the world, only a few species are cultivated as ornamentals. Of these, crape-myrtle (*Lagerstroemia indica*) is probably the most widely planted—mostly in the southern United States where it also occurs as a naturalized shrub. In addition, several members of the genus *Cuphea* are cultivated in greenhouses and open plantings; however, the value of these ornamental species should be discounted by the spread of clammy cuphea (*C. petiolata*) into pastures, meadows, and gardens in southern New England and the Midwest (Fogg 1956). Both of these cultivated genera have tropical affinities, occur south of the probable range of spread of *L. salicaria*, and should not be threatened by biological control agents in northern wetlands. Nor is there a high probability of introduced biological control agents causing damage to native flora. Fernald (1950) listed only 6 genera and 14 species of Lythraceae in central and northeastern North America. *Decodon*, an adjacent genus to *Lythrum*, contains a single species: *D. verticillatus* (swamp loosestrife). This attractive native is probably the most frequent member of Lythraceae to occur in wetlands threatened by *L. salicaria*. *D. verticillatus* is an herbaceous perennial that shows many of the aquatic adaptations of *L. salicaria*. It has woody stems that develop aerenchyma below the water line. It can also spread by setting adventitious roots from stem tips that lodge on moist soil. Swamp loosestrife also has a similar growth form to *L. salicaria*; its stems rise from a central rootstock and reach heights (2.5 m) that equal or exceed purple loosestrife. Swamp loosestrife is not only a highly valued marsh plant, it is one of the few aquatic emergents that seems able to hold back encroaching *L. salicaria* in undisturbed marshes. *Decodon* also seems to have a higher tolerance to shade than does *Lythrum* and therefore is often found growing under wetland forest canopies that would exclude *Lythrum salicaria*. *L. alatum* (winged loosestrife) is another native American *Lythrum* that will need to be considered for the host specificity menu; it is an associate of *L. salicaria* in the wet prairies of the Midwest (Levin 1970). Fernald (1950) described *L. alatum* as extending from Ontario and northern New York to British Columbia, south to Georgia, Louisiana, and Texas; he referred to it as adventive in the Northeast and New Jersey. Bailey and Bailey (1976) described *L. alatum* as "more or less naturalized..." in the northeastern United States. Thus, the northward spread of *L. alatum* may have made the core of its native range vulnerable to biological control agents used against *L. salicaria*. Two other native *Lythrums* (*L. lineare* and *lanceolatum*) are southern in distribution—outside the range of *L. salicaria* infestations. All of these plants should be included in host specificity tests of potential biological control organisms; however, *L. alatum* and *D. verticillatus* should receive special attention since the spread of introduced agents will likely reach their natural habitats.

Susceptibility of Lythrum salicaria *to Biological Control*

Several characteristics of *L. salicaria* make it an ideal candidate for biological control. Its sturdy perennial growth form guarantees that an introduced phytophagous control agent will find a sustained annual production of herbage. If Southwood's (1977) idea of arranging pest species on an r–K continuum is applied, the population dynamics of a mature monospecies stand of purple loosestrife clearly identify the weed as a K-strategist, that is, it "maintains a steady population at or near the carrying capacity of the habitat...." Furthermore, the wetlands occupied by the weed are themselves quite stable and isolated from the traumatic community disturbances that beset plant and insect populations on adjacent croplands. Moreover, the more or less continuous distribution of purple loosestrife along eastern roadsides and waterways creates natural pathways of spread for introduced control agents. The conspicuous floral displays of purple loosestrife also make the plant easy to locate and quantify in surveillance studies.

The distribution of monospecific stands of alligatorweed along waterways in the southeastern United States is similar to the distribution of purple loosestrife in the northeastern and north-central States. In 1965, the successful introduction of a South American flea beetle (*Agasicles hygrophila*) into a dense mat of alligatorweed in northeastern Florida was followed by a rapid expansion of the *Agasicles* population (Spencer and Coulson 1976). In 1966, more than 9,000 *Agasicles* were captured in heavily damaged alligatorweeds near the original release site; these captives were transferred to other alligatorweed infestations in Florida, Georgia, South Carolina, and Mississippi. Spencer and Coulson (1976) noted, "Natural dispersion of the alligatorweed flea beetle occurred rapidly at release sites as the beetles destroyed the alligatorweed. In August of 1976 this ability to disperse resulted in beetles being found as far north as Waycross, Georgia, and at another site some 121 km northwest of the Ortega River release site." It was necessary to introduce two additional South American insects before substantial control was achieved; however, the rapid dispersion of these agents in aquatic and wetland habitats suggests the vulnerability of *L. salicaria* to introduced natural enemies in interconnected wetland complexes in the northern United States and southern Canada.

The lack of aggressiveness of purple loosestrife in western and central Europe suggested to Batra et al. (1986), that these were promising regions to explore for natural enemies of purple loosestrife. They found 120 phytophagous insects attacking *L. salicaria*, and considered 14 of these species to be host specific to *Lythrum* spp. Of these *Lythrum* spp. foragers, they recommended detailed ecological and host-specificity studies for six species: a cecidomyiid fly (*Dasineura salicariae*), whose galling can reduce purple loosestrife foliage by 75% and seed production by 80%; a stem and root boring weevil (*Hylobius transversovittatus*); two chrysomelids (*Pyrrhalta calmariensis* and *P. pusilla*) that can cause nearly 50% defoliation; and two weevils (*Nanophyes marmoratus* and *N. brevis*) that mine ovaries and seeds. Although additional survey work in northern Europe needs to be completed, the results of Batra et al. (1986) indicated that the chances of successful biological control of *L. salicaria* in North America are excellent.

Benefits versus Costs

Before a long biological control effort can be recommended, the costs, risks, and benefits of such a program need to be assessed. Harris (1979) estimated that in Canada the cost of development and implementation of a biological control program for a single weed species was $1.2 to $1.5 million. In the United States, Andres (1977) calculated that the alligatorweed program cost about $1 million as of 1976 with a satisfactory level of control achieved. Andres also estimated that the control of Klamath weed (*Hypericum perforatum*) in California cost $0.5 to $1.0 million with benefits of $40 million (as of 1964) projected for the first 12 years following achievement of control. Our estimate for the cost of a proposed 10-year interagency project on the biological control of purple loosestrife (Table 2) is about $0.5 million. Paralleling the work of the interagency project, Table 2 also lists cooperative efforts that will need to be undertaken by Federal, State, and local governments and various private organizations to carry on the application of an integrated control program. Included here are hidden costs, such as work reassignments to achieve a new field objective under present employment ceilings; new supply, equipment, and travel costs would also be added. We estimate that the cost of these cooperative efforts for the first 10 years would equal the cost of the U.S. Department of Agriculture contract—roughly another $0.5 million. At least 20 States would be beneficiaries of a control program; distributing the costs of the Federal and cooperative programs over a 10-year span would reduce the annual cost per State to $5,000—a fraction of the amount spent on chemical control in several of these States. The USDA's Agricultural Research Service has conducted some preliminary explorations on purple loosestrife (Batra et al. 1986) and is currently funding some additional field studies in Europe by the Commonwealth Institute for Biological Control. Table 2 provides for a year of work to conclude the first phase (Search and Testing) of the 10-year program.

The cost ($1.0 million) of a 10-year biological control program challenges us to show a reasonable prospect of benefits in excess of this proposed expenditure. Recognizing at the outset that we need better information about the quantitative and qualitative damage caused by the invasion of purple loosestrife into a wetland habitat, we nonetheless see several methods of appraisal that will give us some sense of the value of the wetland resource that is threatened.

Wetland Resource Values

All evaluations of wetlands need to be set against the

Table 2. *Schedule and cost estimate for 10-year interagency (USDA-USDI) project on biological control of purple loosestrife (*Lythrum salicaria*).*

Phase	USDA biological control project	Year	Cost	Cooperative efforts by Federal, State, and local governments and private sector, in concert with USDA project
I	Search and testing in Europe for biological control agents	0 + 1	$40,000	During USDA studies in Europe: develop remote sensing techniques for surveillance of *L. salicaria*; measure losses in wildlife and agricultural values following *L. salicaria* infestation.
II	Quarantine and host specificity studies in U.S.	0 + 2	$50,000	During USDA quarantine studies: establish baseline transects for remote sensing of impact and status of *L. salicaria*.
		0 + 3	50,000	
		0 + 4	50,000	
III	Propagation, release, and establishment of biological control agents	0 + 5	$75,000	During USDA release and establishment phase: cooperate with release program; repeat *L. salicaria* transects.
		0 + 6	75,000	
		0 + 7	75,000	
IV	Monitoring and evaluation studies	0 + 8	$30,000	During USDA evaluation studies: repeat *L. salicaria* transects; support USDA monitoring and followup.
		0 + 9	30,000	
		0 + 10	30,000	
Total USDI contribution to USDA			$505,000	

background of the destabilization and continued shrinkage of this resource. Shaw and Fredine (1956) examined the fate of wetlands in California, Florida, and five central midwestern States. From an 1850 base of 15 million ha, wetlands within these States were reduced by 9.3% in 1906, 33.2% in 1922, and 45.7% around 1955. These values are distinctly lower than the shrinkage estimate we have given earlier (66%) from Auclair's studies in southern Wisconsin; however, Auclair's method was based on land survey data and was outside the area sampled by Shaw and Fredine. In addition to drainage and cultivation, Jaworski and Raphael (1979) pointed to the reduction in diversity and biological stability of remaining wetlands as a problem that has not been adequately studied.

Methods of evaluation. Methodologies for evaluating wetlands described in a symposium on wetland functions and values (Greeson et al. 1979) included a hierarchical approach (Odum), nonconsumptive uses (Reimold and Hardisky), and social values (Foster). Linder and Hubbard (1982) discussed wetland values in the prairie pothole region. We have chosen to use three appraisal methods to lend perspective to the value of wetlands threatened by purple loosestrife. We have also limited our evaluations to 12 eastern and 7 north-central States where *L. salicaria* has already demonstrated its potential for widespread habitat degradation.

Realty value. Table 3 presents Shaw and Fredine's (1956) estimates of the distribution of four freshwater wetland types in 12 States that compose the Atlantic Flyway North and 7 States that make up the Mississippi Flyway North. All four of these wetland types are more or less vulnerable to invasion by *L. salicaria* but, for our purposes, we will include only Types 3 and 4 wetlands—the shallow and deep marshes that are especially susceptible to infestation and are prime waterfowl habitats. Cowardin et al. (1979) have criticized Shaw and Fredine's estimates as being conservative, but until more accurate assessments are available, these estimates best suit our needs. If we use $750 (R. Erickson, North Central Region, USFWS, personal communication) as a modest estimate of the value of a hectare of shallow or deep freshwater marsh, the realty value of 499,000 ha threatened by *L. salicaria* in the Atlantic and Mississippi flyways (north) is $374 million.

Fur harvest. The dependence of the muskrat on broad-leaved cattail for food and cover marks the productivity of this fur crop as threatened by the expansion of purple

Table 3. *Area (hectares) of four freshwater wetland types in the northern zones of the Atlantic and Mississippi flyways.*[a]

Wetland type	Atlantic Flyway North	Mississippi Flyway North
1. Seasonally flooded basins	480	453,600
2. Inland fresh meadows	12,280	953,320
3. Inland fresh shallow marshes	14,360	303,400
4. Inland deep fresh marshes	10,280	171,080
Total fresh wetland	37,400	1,881,400

[a] From Shaw and Fredine (1956).

loosestrife. From the work of Deems and Pursley (1978) we extracted data on the harvest of muskrat fur from the 19 States that make up the northern zones of the Atlantic and Mississippi flyways (Table 4), and calculated that the mean annual value of pelts taken from 1970–71 to 1975–76 was $13,982,133. The mean annual price per pelt was $2.69.

Migratory bird hunting expenditures. The amounts of money people spend in pursuit of recreation have been generally accepted as a valid estimate of the resource base

Table 4. *Muskrat fur harvest and honey sales from the Atlantic Flyway North and Mississippi Flyway North.*

State	Fur value in $ (thousands)[a]	Honey sales in $ (thousands)[b]
Atlantic Flyway North (*n* = 12)		
Maine	133	36
New Hampshire	22	1
Vermont	385	58
Massachusetts	144	39
Rhode Island	7	—
Connecticut	7	12
New York	385	1,456
New Jersey	1,760	93
Pennsylvania	1,099	266
Maryland	613	26
Delaware	177	—
West Virginia	134	79
Subtotal	4,866	2,066
Mississippi Flyway North (*n* = 7)		
Ohio	1,698	402
Indiana	853	144
Illinois	1,197	242
Iowa	1,204	1,428
Michigan	937	1,538
Wisconsin	1,698	2,440
Minnesota	1,528	4,560
Subtotal	9,115	10,754
Total	13,981	12,820

[a] From Deems and Pursley (1978).

[b] From 1974 Census of Agriculture (USBC 1977*a*).

that supports the activity. We used regional summaries of the 1980 national survey of outdoor recreation (USFWS and USBC 1982) to calculate that 0.5 million migratory bird hunters in the 19 northeastern and northern midwestern States spent an average of $120 per year, or a total of $65.6 million on their sport. Included in this total were hunters who sought geese (about 1/3), woodcock (about 1/10), and doves (<1/10); since these birds are not often found in marsh habitat, we have halved the total migratory bird hunting estimate to $32.8 million.

Outdoor recreation expenditures. Increasing numbers of nature enthusiasts find fulfillment in outdoor settings. Their activities and expenditures have been compiled as "nonconsumptive wildlife use" (USFWS and USBC 1982). Again, we calculated from regional summaries that 12.6 million participants spent $129.86 annually, for a total of $1,639 million. These people traveled away from their residences for the primary purpose of observing or photographing native animals in their natural habitats. About 1/10 of the sites visited were marsh or wetland, hence we computed that the annual expenditure for viewing marsh or wetland wildlife was $163.9 million.

Benefit–Cost Ratio

From the preceding estimates of wetland resource values we constructed a benefit–cost analysis (Table 5) of the proposed biological control program on purple loosestrife. At the outset, we grant that a benefit–cost analysis is difficult to apply to a resource whose output is primarily aesthetic, that is, promotes a feeling of well being. About 86% of the resource value that we were able to identify in Table 5 was based on the amounts of money spent in pursuit of outdoor recreation. Among gains (benefits) we have listed, the annual value of

Table 5. *Benefit-cost analysis of resources and values at risk to purple loosestrife infestation versus costs of a 10-year biological control program.*[a]

Benefit–cost	Annual value in $ (millions)
Gains	
Realty value of threatened wetlands ($374 million amortized at 5% for 20 years)	18.7
Wild hay and pasture	no estimate
Fur harvest (muskrat)	14.0
Migratory bird hunting expenditures	32.8
Wildlife observation and photography	163.8
Annual resource value	**229.3**
Biological control saves 20%[b] of annual resource value	× .20
Total annual benefit	**45.9**
Losses	
Combined cost of biological control[c]	0.1
10% of annual honey sales in 19 States[d]	1.3
5% of annual sales of herbaceous ornamentals[e]	0.3
Total annual cost	**1.7**

Benefit–cost ratio = 45.9/1.7 = **27.0**
Estimated 27 units of benefit for each unit of cost

[a] Applied to 12 northeastern States and 7 northern Midwest States whose wetlands have been invaded by *L. salicaria*.

[b] Projected for 20 years with 75% reduction in weed densities assumed at end of 10-year biological control program.

[c] Includes $0.05 × 10^6 for USDI contract (Table 2) plus $0.05 × 10^6 for workload reassignments and other costs to Federal, State, and local governments and private sector.

[d] From USBC 1977*a*.

[e] From USBC 1973.

wetland habitat was determined by the current price per hectare amortized at 5% over 20 years. This is a conservative estimate, in that land seldom sells for as little as $750/ha ($300/acre). Moreover, wetlands often occur as neglected swales in a surrounding matrix of farm, range, forest, or residential tracts—making them difficult to purchase or manage as productive wildlife habitat. Although the 1974 Census of Agriculture (USBC 1977*b*) listed 24,764 farms cutting a wild hay crop valued at $13.0 million, we were not able to identify that portion cut in marshes or riparian meadows. The annual fur statistics used to estimate this resource came from a set of years (1971–76) that included low to moderate (but not high) pelt prices.

To give reasonable balance to our calculation of the benefits to be derived from biological control, we postulated that an acceptable result at the end of the 10-year program would be a 75% reduction in the overall densities of the weed, thereby saving 20% of the annual resource value. The projection of a 20% saving assumes that reductions in purple loosestrife densities cannot be expected to begin until the 7th year of the program. Even if dramatic reductions are achieved by the 10th year, substantial savings in resource value would not accrue until the second decade. Moreover, in the worst situation, if *L. salicaria* were to continue spreading at an unchecked rate, total resource value would not fall below some unknown minimum. In estimating costs or losses of biological control, we listed the annual cost of the interagency project ($0.5 × 10^6) and also an equal amount to cover hidden costs among many levels of cooperators who will participate in field activities. In our allowance for loss of nectar and pollen forage that might accompany biological control of *L. salicaria*, we note that Iowa, Michigan, Minnesota, and Wisconsin account for 78% of annual honey sales from the 19 northeastern and northern midwestern States (Table 4). Since wetlands in these States are less than half colonized by purple loosestrife (Fig. 19), we believe our estimate of potential loss to be fair. A Wisconsin honey producer (J. Mills, per-

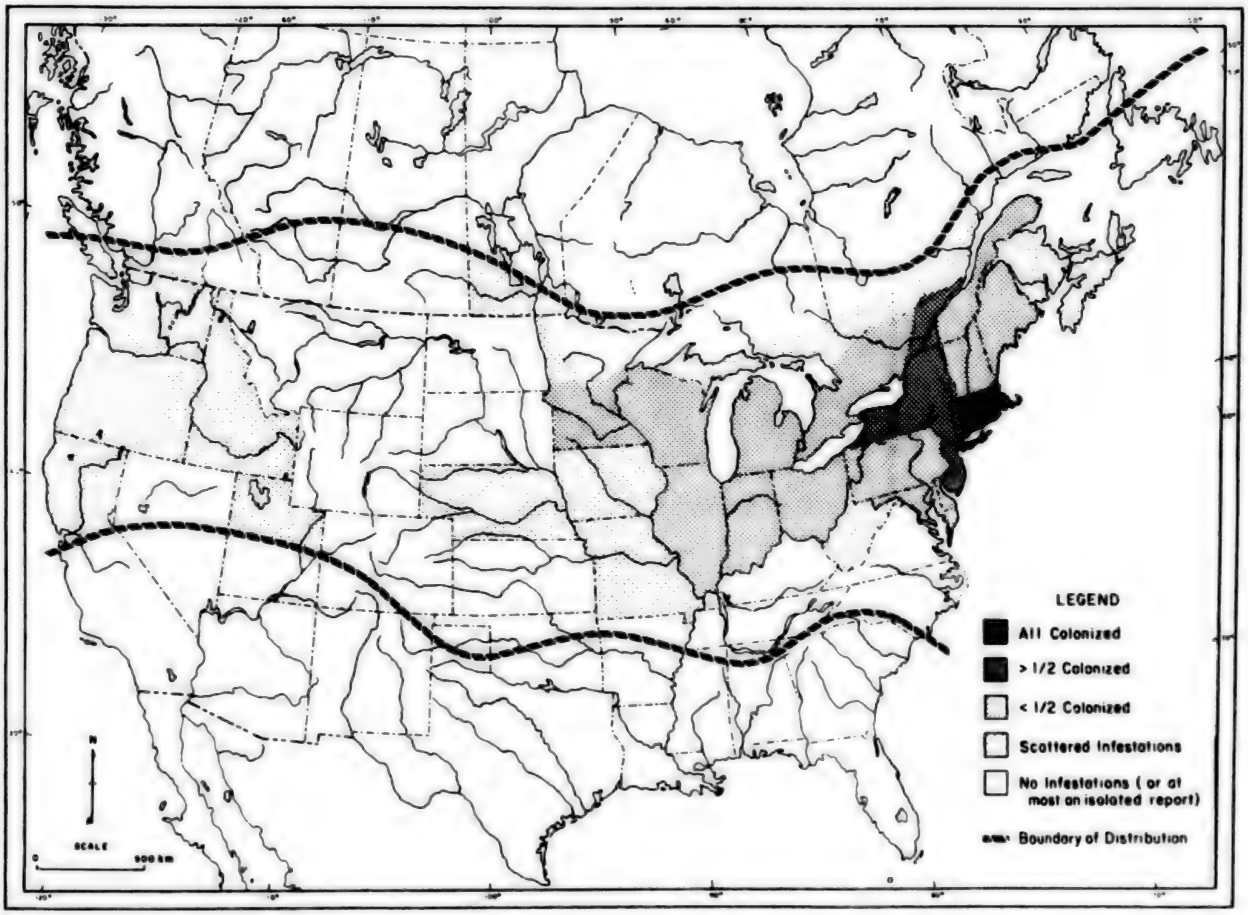

Fig. 19. Status of *Lythrum salicaria* infestations in North American wetlands as of 1980.

sonal communication) advised us that although purple loosestrife was often useful forage for hives that were being "hardened" for winter, it was not important in honey production. We were not able to obtain an accurate estimate of the value of nursery stock (infertile cultivars of *L. salicaria*) that might be damaged by biological control organisms. Total nursery sales of herbaceous ornamentals in the United States in 1970 were $6,045,661 (USBC 1973). Purple loosestrife makes up some small part of this total; we doubt that it exceeds 5%.

In summary, we conclude that a conservative projection of the benefit–cost ratio of a biological control program would yield at least 27 units of benefit for each unit of cost. As indicated earlier, we confined our analysis to the eastern half of the United States where *L. salicaria* has already shown that it can invade and displace native marsh vegetation.

Other Risks and Rewards

In addition to the cost of operating a biological control program, we need to consider other ecological and economic risks that would accompany these efforts against purple loosestrife. The primary risk for natural resource managers would be that an introduced organism might alter its behavior in its new environment or have some unanticipated secondary effect that would be ecologically damaging to the native biota. Serious ecological damage probably occurred in the history of biological control in Hawaii. Zimmerman (1958) noted, "Swezey was the last of the entomologists to have seen many of the endemic Hawaiian Lepidoptera in a semblance of their natural abundance. The importation of parasites to control various moths of economic importance, together with the accidental importation of other parasites has resulted in wholesale slaughter and near or complete extermination of countless species. . . . Many are forever lost."

Another critic from Hawaii (Howarth 1983) declared his alarm that reviews of biological control have implied that the method was without environmental risk and observed, "Once the target pest appears adequately controlled researchers have turned their attention to other pests." He softened his argument by acknowledging that there have been extremely limited funds for research on the impacts of biological control introductions, and noted that the Hawaii State Department of Agriculture has begun including vulnerable native arthropods in the testing protocol for candidate biological control species. The difficulties of designing and executing field studies that would adequately monitor the impact of introduced species caused Simberloff (1985) to observe, "estimates of no effect are actually estimates of no obvious, dramatic effect." In reviewing the record of biological control, Buckingham (1984) granted that the method can never be declared absolutely safe, but cited an 80-year summary (Julien 1982) of 192 biological control agents (mostly insects) that had been used against 86 weed species without unleashing an important pest. Buckingham also noted that as ever more restrictive measures are added to assure safety (especially tests for possible damage to native plants) many potentially beneficial agents must be dropped from consideration or have their clearance unduly delayed.

To balance these ecological risks, the stress of spraying herbicides on wetland habitats would be eased by a biological control program. The high costs of product development have dictated that herbicides used on wildlife habitats be formulated from chemicals developed for application on relatively simple agricultural ecosystems. The application of a broad-leaved herbicide to a monocot crop or a pine plantation can handily achieve the manager's goal of suppressing competition from dicot weeds, but it is a mistake to apply such a simple treatment to a natural wetland that may support a complex of more than 100 species occupying several photosynthetic levels and supporting a fauna living at many trophic levels. From the viewpoint of healthy species diversity, the use of a broad-spectrum herbicide (glyphosate) is an even more drastic blow to a wetland community. Indeed, continued spraying of wetlands with herbicides will tend to shift survivorship of community members to resistant species. A second benefit from biological control would be savings on the cost of applying chemicals to wetlands infested with purple loosestrife. We estimate that the annual cost of spraying herbicides (principally 2-4,D and glyphosate) on purple loosestrife in the Northeast and northern Midwest exceeds $75,000.

On balance, the decision to apply (or not to apply) biological control to purple loosestrife hinges on weighing the uncertainty of a minor risk of environmental damage against the certainty of continued degradation of North American riparian and wetland habitats by this weed. The greatest problem facing the initiation of a biological control program is the widely scattered responsibilities and proprietary interests at private, State, Provincial, national, and international levels. Nevertheless, other weed threats have affected a wide array of potential beneficiaries and have been successfully confronted with interagency and international agreements, namely, alligatorweed (Spencer and Coulson 1976), water hyacinth (Wright and Center 1984), and musk-thistle, *Carduus nutans* (Linehan 1982).

Purple loosestrife was approved as a candidate for biological control by an interagency committee in 1980. As of this writing, an interagency agreement between the USDA and USDI has received favorable review; Federal funds for 1986–87 have been appropriated.

Conflict Resolution

DeLoach (1978) recognized that the generally beneficial effects of biological control programs can also have negative economic or ecological impacts on nontarget organisms. Andres (1980) suggested some guidelines for the resolution of these conflicts. He also pointed to the need for improved methods of predicting the effects of biological agents on nontarget plants. We are aware of three potential conflicts that may result from the decimation of *L. salicaria* by an introduced biological agent.

Honey Production

Although a successful biological control program would further reduce *L. salicaria*'s minor role as a nectar source, an analysis of the 10 leading honey-producing States in 1974 (Table 6) shows that none of the top producers have high acreages of loosestrife infestation (Fig. 19). Minnesota and Wisconsin have very large areas of glacial marsh, but less than half of these wetlands are colonized by purple loosestrife. A further analysis of honey production in these top 10 States shows that they contain 34% of the Nation's farms with bee colonies and 65% of the national total of colonies; they also account for 68% of national honey sales. These data reflect the migratory pattern of large honey producers. They winter their colonies in southern States and move them north each spring in search of foraging areas. Nevertheless, to the small honey producer in the Northeast and north-central United States, the prospect of additional losses of bee foraging plants is difficult to face. Since the advent of carbaryl insecticides, northeastern and north-central beekeepers have sought wetland foraging areas for relief from inadvertent mortality caused by insecticides applied to upland forage crops.

The resolution of this conflict might turn on the realization that a successful biological control program would not seek the extermination of purple loosestrife. A 75% reduction in the density of purple loosestrife would probably allow wetland managers to cope with the species; surviving *L. salicaria* would provide a substantial base of pollen and nectar forage amidst a healthier mix of native plants. The *American Bee Journal* has already opened its pages to proponents of both sides of this conflict (Bunch 1977*a*, *b*; Hayes 1979; Hughes 1977; USFWS 1979). This is a wholesome beginning.

Horticultural Sales

Several aspects of the sales of horticultural stocks of *Lythrum* spp. need to be considered. First, the annual

Table 6. ***Number of colonies of bees and value of honey on farms with sales of $2,500 or more in top 10 honey-producing States.***[a]

Rank	State	Inventory of colonies		Honey sales
		No. of farms	No. of colonies	($1,000)
1	California	447	305,753	8,137
2	South Dakota	91	115,904	4,505
3	Idaho	104	106,376	3,178
4	Minnesota	237	103,222	4,560
5	Washington	157	97,655	1,816
6	Nebraska	150	98,877	3,667
7	Texas	368	77,717	2,651
8	Florida	174	75,338	2,339
9	Wisconsin	435	70,330	2,440
10	North Dakota	53	61,552	2,926
Total		2,216	1,112,724	36,219
U.S. Total (48 States)		6,459	1,708,383	53,614

[a] From 1974 Census of Agriculture (USBC 1977*a*).

national sales of purple loosestrife are probably a minor item compared with the environmental costs imposed by the inadvertent escape of wild-type stock into adjoining wetlands. Although they make very attractive perennial displays, the various cultivars of *Lythrum* are not a significant part of the annual sales of nursery products. Total nursery sales of all herbaceous ornamentals in the United States in 1969 were estimated at $6,045,661 (USBC 1973). *Lythrum* stock was not important enough to be identified. Second, a ban on the shipment and sale of *Lythrum salicaria* should not block the growth and sale of infertile hybrid stock. Examples of infertile hybrid stock that we have seen have small, delicately set leaves and flowers in greatly elongated inflorescences that do not produce seed capsules. Third, most landscape settings that include infertile hybrid stock would be far enough removed from wetland habitats to screen the plantings from the full impact of control agents. Moreover, a protective insecticide spray program could probably be developed to reduce damage to an acceptable minimum.

Recent actions of the Minnesota Nurseryman's Association (B. Harper, personal communication) have demonstrated that they are anxious to participate in a resolution of this potential conflict. Other states would do well to follow their responsible example.

Containment Strategy and Tactics

If preliminary work on a biological control program were to continue, it would be 5 or 6 years under the most favorable circumstances before a release program could be started. With a few delays, it could be 8 or 10 years before relief could be expected from local purple loosestrife infestations. In the interim, containing the spread of existing infestations is obviously the best approach. As a background for containment strategy, we have constructed a map (Fig. 19) that displays the extent and intensity of purple loosestrife infestations across North America in 1980. We have defined "infestation" as one or more mature plants in each wetland unit or drainage basin. Within the past 15 years, the senior author has traversed sections of most of the States and Provinces within the boundaries of infestation during *L. salicaria*'s period of bloom. A log of roadside sightings of purple loosestrife was kept; field observations and photographs were made of infestations of special interest. These observations, correspondence with other field observers, and botanical records compiled by Stuckey (1980) are the basis for the infestation map. The north and south boundaries of spread are intended to define the approximate limits within which *L. salicaria* can be expected to expand. There are already collection records or reports outside of these limits, but the rate of spread from these isolated sites has been slow. The probabilities of continued spread northward in British Columbia and southward in the lower Central Valley of California are particularly difficult to judge.

A useful perspective can be gained by noting the inverse relation between *L. salicaria* infestations (Fig. 19) and the distribution of wetlands in the northeastern and midwestern United States (Table 3). The four wetland types listed in this table are of prime importance in waterfowl and shorebird production. Totals for the Atlantic Flyway North versus Mississippi Flyway North are 37,400 and 1,881,400 ha, respectively; these estimates are adequate to underscore the need for prompt action in checking the westward expansion of purple loosestrife. The northeastern United States wetlands that are now almost completely colonized represent but a small fraction of the wetland resource at risk in the north-central States. The impact of *L. salicaria* on one of our major waterfowl areas (Mississippi Flyway North) will be determined within the next 10–20 years. The Central and Pacific flyways are as yet unaffected by purple loosestrife.

Minimizing Spread and Impact

The concept of classes or levels of infestation is useful in evaluating containment or control tactics. Table 7 characterizes three stages in the development of a local infestation. Obviously, these stages vary with the dynamics of each site. It is wise to keep the logistic curve in mind when judging the age of an infestation. The slow growth of biomass in Class I gives the landowner or manager the best opportunity for control or eradication. Class II infestations are possible to control, but the investment in effort and chemicals has roughly trebled. Class III infestations may be in a phase of exponential increase and are the most difficult and expensive to control.

Early Detection

Although a stubborn and aggressive weed, *L. salicaria* has two characteristics that can be readily exploited to slow its spread and impact. First, its tall, showy, floral stalks and prolonged period of bloom immediately identify an established plant. Second, the rate of spread of purple loosestrife in undisturbed habitats is slow. Seeds or propagules falling from the parent plant need moving water (or surface drift) to expand into surrounding

Table 7. *Purple loosestrife infestation classes.*

Class	Age (years)	Growth form	Percent of biomass
I	1–3	Scattered small plants with 1–5 flowering stems per rootstock.	<5
II	3–5	Mature plants with 10 or more flowering stems per rootstock. Clumps sometimes coalescing and forming aggregate floral masses.	10–20
III	5 or more	Aggregates closing to form large monospecific patches or strands.	>30

habitat. They also need to find a patch of moist soil that is exposed to sunlight to establish themselves as seedlings. Moreover, these conditions must prevail for about 50 days to allow the seedlings to grow to sufficient size to survive over winter. If an isolated adult plant has somehow become established in an otherwise healthy wetland, its seeds will fall in a 10-m-long ellipse on the downslope or downwind side of the plant, where they will remain viable for at least 3 years. If the emergent vegetation around the invader remains vigorous and undisturbed, the spread of these seedlings will be very slow. Managers whose units are within the limits of purple loosestrife distribution would do well to include an annual search for purple loosestrife in their work schedules. The search need not be highly organized or exclusively pursued, but it is important that it remain among each summer's plans. The blooms on mature plants are brightest and most obvious during July; however, the surveillance should be continued into the last half of the bloom season (August) when year-old plants or exceptionally vigorous seedlings of the current growing season may come into bloom. A 20-power spotting scope is useful for identifying floral stalks in large reaches of open marsh. The most likely wetland sites for the appearance of purple loosestrife are along water supply entrances, or on any disturbed area within the upper flood contour. Muskrat houses, old tree stumps, exposed bottom deposits, new dike or road fills, boat ramps, and duck blinds are likely sites for a drifting or transported loosestrife propagule to set roots. If there are infested pools or waterways adjacent to the management unit, crossings or pullovers by muskrats or snapping turtles are also possible routes of entry for purple loosestrife seeds.

Local Eradication

Early detection of the arrival of purple loosestrife is essential to successful local control. If the wetland management unit is completely circumscribed by dikes, roads, or other barriers to drift of local seed sources, the manager can successfully follow a program of local eradication. The first appearance of invading *L. salicaria* is usually a few scattered plants. A small field crew should be sent to these sites with instructions to dig or hand pull all purple loosestrife plants, including the root crown. Since fragments of purple loosestrife can reproduce vegetatively, it is important to carry all pulled material out of the marsh basin. If the plants are several years old, they will be too large and deep-rooted to be removed. In this event, a hand sprayer should be used to apply an herbicide directly on the leaves. Great care should be taken to avoid drift onto the weed's nearest neighbors; these plants are needed to close in the space occupied by the dying loosestrife clump. Spraying with glyphosate can be done any time after loosestrife foliage is well developed; however, Rawinski (1982) obtained best results with August sprays. If seedlings are established in the vicinity of the parent plants, herbicides should be applied and the area marked for continued treatment. With diligent followup and continued surveillance, local eradication is feasible. L. S. Smith (personal communication) was successful in eradicating *L. salicaria* from the Iroquois NWR in the early 1960's.

Coping with Infested Areas

If *L. salicaria* is well established within the management unit and several years of seed production have occurred, the opportunity to attempt local eradication has probably been lost. The unit is vulnerable to heavy infestation and wetlands managers must be cautious in exercising their options. If the area of infestation is concentrated and funds are available, the manager could embark on a salvage program. Spraying with glyphosate from air or by boat is the only effective means of delivery that does not physically damage the habitat; however, many pitfalls must be avoided in an aggressive control program. The high cost of aerial spraying with glyphosate makes chemical control over large marsh units impractical, especially if loosestrife clumps are scattered among areas of undisturbed native cover. Spraying of purple loosestrife interspersed in willow, dogwood, or other marsh shrubs should be avoided since these woody plants have the ability to shade out purple loosestrife as their canopies close. Carefully handled, and in concert with intensive work by field crews, spraying with glyphosate or other chemicals can be a successful tactic in the local control of purple loosestrife. This tactic, however, does nothing for the vast areas of purple loosestrife that are not under intensive management. These remain a constant seed source that can only be checked with a national strategy, that is, a biological control program.

Until a biological control program can be implemented, the key to coping with established *L. salicaria* is to avoid any manipulations or actions that might stress the native vegetation and allow *L. salicaria* seedlings to spring up from dormant seed stocks. The standard waterfowl management practice of early drawdown to encourage smartweed (*Polygonum* spp.) and millet seedlings on shallow impoundment margins is an open invitation to purple loosestrife dominance. Shallow midsummer flooding to provide dabbling duck foraging will often not be sufficiently deep to suppress young loosestrife seedlings. If reflooding is delayed by multiple stage coverage, seedlings may grow tall enough to survive as emergent aquatic plants.

If, for example, a water control structure must be repaired, drawdown should be delayed until mid-July. The peak of the growing season will have passed and *L. salicaria* seedlings will not have had sufficient time to become well established. If an early drawdown cannot be avoided, reflooding with at least 70 cm of water will kill most first-year plants.

Last, any form of disturbance or stress to the native plant community should be avoided. As suggested earlier, the shaded understories of wetland hardwood forests or shrub–carr stands will exclude *L. salicaria*. However, if these stands are flooded for more than half of their normal growing season, they will begin to die and purple loosestrife will become established as openings appear in the forest canopy. Similarly, the use of heavy equipment in open marsh that has been colonized by purple loosestrife will greatly favor the dominance of the weed. *L. salicaria* has the ability to reproduce from adventitious buds growing from crushed stem segments, whereas many of its native associates (*Typha* spp., *Scirpus* spp., and *Phalaris arundinacea*) do not survive crushing.

Moist Soil Management

Manipulating wetland edge soils is an effective habitat enhancement technique in southeastern Missouri (Fredrickson and Taylor 1982). Moist soil management involves discing or scarifying the topsoil to encourage the establishment of seedlings or propagules of desirable food or cover plants. The site is then flooded for part or all of the growing season and later exposed with a gradual drawdown. Depending on tactical goals, drawdowns could begin in April, or be delayed until August, with corresponding adjustments in the time of drawdown. Although moist soil management is usually practiced on sites that can be worked with power equipment—and therefore can be cultivated to control purple loosestrife—great caution should be exercised in using this technique in the presence of purple loosestrife. Moist soil regimens that use early drawdowns (first half of the growing season) will favor the establishment of purple loosestrife; on these sites the cost of *L. salicaria* control will probably outweigh the benefits of enhancement.

Control in Pastures, Roadsides, and Ditches

The perennial growth pattern of *L. salicaria* makes it susceptible to control by plowing or discing wherever these methods are feasible and cost effective. Spraying with glyphosate is also an effective control measure on ditchbanks or along roadsides that can be reached with power equipment.

Weed Control Law

Plant Quarantine

For the wildlife manager, the basic problem with weed control laws is that they are aimed at agricultural pests and are enforced by State and Federal agencies whose mission (as it should be) is protection of food and fiber crops. Purple loosestrife is not the first weed that primarily impacts fish and wildlife values (water hyacinth and alligatorweed are among previous examples in the subtropics), but it is surely the first weed that has threatened to dominate millions of hectares of temperate marsh and open riparian habitats across the continent. We are caught without effective laws or institutions to cope with this weed. Although Federal plant quarantine laws are of little use once an immigrant plant has become naturalized, State laws and enforcement could be very effective in shutting down the shipment of wild-type purple loosestrife as horticultural stock. These laws may be seen as a threat to wholesale suppliers, but if their stocks are truly infertile hybrids, they have nothing to lose but competition from less scrupulous suppliers. Amendments to existing State quarantine regulations should exempt infertile stock from quarantine. The identification of nursery stock may be an enforcement problem, but the key point should be bona fide infertility. This would have to be tested in trial plantings from time to time. Some sort of cooperative enforcement agreements between fish and wildlife enforcement officers and State plant quarantine authorities would need to be set up; similar arrangements are already in place to screen importations of wild animals at international air terminals.

Transportation and Sale of Seeds

The Federal Seed Act of 1939 (Robbins et al. 1942) regulates the transport and sale of seeds in foreign and interstate commerce. Although there is little likelihood of purple loosestrife occurring in grain or forage seed shipments, Wade (1983) showed that it is present in seed mixes offered by various wild plant suppliers. These sources of impure seed would need both Federal and State regulations to control. Pure seed regulations would also be a useful means of curtailing the sale of purple loosestrife seeds by apicultural suppliers.

Noxious Weed Status for Purple Loosestrife

Declaring purple loosestrife a noxious weed is a State-level strategy that is often highly effective. This action has already been taken by California, Idaho, and Ohio; three other States (Minnesota, Illinois, and Wisconsin) are considering similar action. Noxious status usually places the species under the State's pure seed surveillance and plant quarantine. In addition, most States have enabling legislation in place that provides for the establishment of weed control districts by landowners. Herein lies a potential conflict between agricultural and wildlife interests. The local weed board has the power to issue warnings to the managers of private and public lands that they must control noxious weeds on their land. If action is not taken by the landowner, the weed board has the right to send in their own spray crews and bill the landowners for the cost. The stress of systemic herbicides on natural vegetation plus the ruts and crushed plants caused by off-road spray rigs could have disastrous effects on the health and productivity of a wetland habitat. The Nebraska Game and Parks Commission estimates that it pays $45,000 each year for unwanted spraying (mostly for Canada thistle [*Cirsium arvense*] and musk-thistle [*Carduus nutans*]) on their Fish and Wildlife Management Areas (C. McLain, personal communication, 17 December 1982). The Nebraska Game and Parks Commission is well aware that in addition to obligatory spraying costs, their greatest loss may be the unintended impact of spraying on native wildlife food and cover plants. Perhaps an early understanding between local conservation officials and the district weed board could avoid these misdirected and unfortunate efforts. Nevertheless, we believe far more is to be gained by seeking noxious weed status for purple loosestrife than by avoiding possible conflicts and thereby losing the chance to enter the plant into existing weed control enforcement programs.

Integrated Pest Management

Integrated Pest Management (IPM) is a useful approach in that it attempts to view pest problems from a holistic and cohesive perspective. IPM has been described by Bottrell and Smith (1982) as "a systems approach to reduce pest damage to tolerable levels through a variety of techniques, including natural predators, pathogens, parasites, genetically resistant hosts, environmental modifications, and, when necessary and appropriate, chemical pesticides. Generally, IPM programs first use nonchemical defenses against pests before altering the environment with chemical pesticides." This concept has been developed by agricultural scientists with the view of controlling pest species with combinations of methods that would be most cost effective and least damaging to the agro-ecosystem. Schreiber (1982) used computer modeling to describe the structure and function of the pest species environment. Batra (1982*a*) underscored the holistic approach of IPM in her listing of the sequence of methods used from the least to the most disturbing to the ecosystem. The first methods listed are variations of biological control; the remaining methods apply increasingly stiff and costly impacts on the agro-ecosystem—ending with chemical control and various cultural controls, such as, tillage, mowing, and plowing. The application of successive levels of IPM requires estimates of the degree of "economic damage" caused by the pest. Recognizing that the estimation of "economic damage" poses some problems in wildlife areas, nature preserves, or parklands, we suggest that the basic goals of IPM are even better suited to natural habitats than to agro-ecosystems. Thus far, the application of IPM to wildlife habitat has included range weeds on Great Plains wildlife refuges (Linehan 1982) where Service biologists and refuge managers cooperated with biological control efforts against musk-thistle and goatweed (*Hypericum per-*

foratum) using a snout-weevil (*Rhinocyllus conicus*) and other beetles (*Chrysolina* spp.), respectively. The last phases of a biological control program for purple loosestrife could be readily worked into an IPM system in concert with State, Provincial, and national wetland resource agencies.

Research and Information Needs

The recent spread of purple loosestrife into Nebraska and Wyoming (Thompson and Yates 1985) completes a cross-continent distribution, and demonstrates that this weed is a problem of national importance. Since dollars for research and control depend on solid evaluations of economic loss, one of the first needs is for studies that demonstrate and quantify actual losses incurred with infestations of *L. salicaria* in natural and agricultural habitats. Meanwhile, the spread and expansion of the weed's geographic range should continue to be monitored. Best et al. (1981) demonstrated that 10 species of hydrophytes (4 of them *L. salicaria* associates) can be identified with remotely sensed imagery. This and other inventory techniques should be applied to purple loosestrife. We also need to know much more about the growth, reproduction, and survival of purple loosestrife in relation to its plant associates so that wetland managers can better work within the constraints imposed by the invasion of this weed. Although special formulations for glyphosate and other wide-spectrum agricultural herbicides have been approved for wetland and aquatic use, we know little about the impact of these chemicals on wetland and aquatic plant communities. We also need to test various infertile cultivars of purple loosestrife to verify that these horticultural clones remain sterile under a wide range of sites and conditions. Last, we should continue work on the search for biological control agents in Europe. An interagency biological control program is potentially the most cost-effective and least environmentally damaging control tactic that can be devised.

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References

Ahrens, J. F. 1974. Selectivity of glyphosate and asulam in ornamental plantings and Christmas trees. Proc. Northeast. Weed Sci. Soc. 28:361–368.

Altschul, S. von R. 1973. Drugs and foods from little known plants, notes in Harvard University herbaria. Harvard University Press, Cambridge, Mass. xii + 366 pp.

Andres, L. A. 1977. The economics of biological control of weeds. Aquat. Bot. 3:111–113.

Andres, L. A. 1980. Conflicting interests and the biological control of weeds. Proc. Int. Symp. Biol. Control Weeds, Brisbane, Australia. 5:11–20.

Anonymous. 1847. Annals of horticulture. Page 153. Houlston and Stoneman, London.

Anonymous. 1944. 1—Purple loosestrife. Am. Bee J. 84:57.

Auclair, A. N. 1976. Ecological factors in the development of intensive-management ecosystems in the midwestern United States. Ecology 57:431–444.

Bailey, L. H., and E. Z. Bailey. 1976. Hortus third. Macmillan Publishing Co., Inc., New York. xiv + 1290 pp.

Baird, D. D., R. P. Upchurch, W. B. Homesley, and J. E. Franz. 1971. Introduction of a new broadspectrum postemergence herbicide class with utility for herbaceous perennial weed control. Proc. North Cent. Weed Control Conf. 26:64–68.

Balogh, G. R. 1986. Ecology, distribution, and control of purple loosestrife (*Lythrum salicaria*) in northwest Ohio. M.S. thesis, The Ohio State University, Columbus. xiv + 107 pp.

Batra, S. W. T. 1982*a*. Biological control in agroecosystems. Science 215:134–139.

Batra, S. W. T. 1982*b*. Biological control of weeds: principles and prospects. Beltsville Symp. Agric. Res. 5:45–59.

Batra, S. W. T., D. Schroeder, P. E. Boldt, and W. Mendl. 1986. Insects associated with purple loosestrife (*Lythrum salicaria* L.) in Europe. Proc. Entomol. Soc. Wash. 88:748–759.

Batt, B. D. J., J. A. Black, and W. F. Cowan. 1980. The effects of glyphosate herbicide on chicken egg hatchability. Can. J. Zool. 58:1940–1942.

Bent, A. C. 1921. Life histories of North American gulls and terns. U.S. Natl. Mus. Bull. 113. x + 333 pp.

Best, R. G., M. E. Wehde, and R. L. Linder. 1981. Spectral reflectance of hydrophytes. Remote Sens. Environ. 11:27–35.

Bodmer, H. 1928. Beiträge zur anatomie und physiologie von *Lythrum salicaria* L. Beih. Bot. Zbl. 45:1–58.

Bodrogkozy, G., and I. Horvath. 1977. Connection between stand pattern and the organic matter production in the marshlands of the inundation area at Kortvelyes. Tiscia 12:65–70.

Bodrogkozy, G., and I. Horvath. 1979. Effect of lasting floods on the species composition and organic-matter production of the marshy meadow-lands in the floodplains of the Tisza. Tiscia 14:81–88.

Boggs, K. D. 1932. Prints and plants of old gardens. Garrett and Massie Publishers, Richmond, Va. x + 101 pp.

Bottrell, D. G., and R. F. Smith. 1982. Integrated pest management. Environ. Sci. Technol. 16:282A–288A.

Brown, A. 1878. Plants introduced with ballast and on made land. Bull. Torrey Bot. Club 6:255–258.

Brown, F. J., and J. S. Roucek, editors. 1945. One America. Rev. ed. Prentice-Hall, Inc., Englewood Cliffs, N.J. vii + 717 pp.

Brown, J. L., and N. R. Spencer. 1973. *Vogtia malloi*, a newly introduced phycitine moth (Lepidoptera: Pyralidae) to control alligatorweed. Environ. Entomol. 2:519–523.

Buckingham, G. R. 1984. Biological control of weeds by insects. J. Ga. Entomol. Soc. 19(3/2nd suppl.):62–78.

Buist, R. 1852. American flower-garden directory. A. Hart, Philadelphia. xvi + 339 pp.

Bunch, Q. 1977*a*. Purple loosestrife—a honey plant. Am. Bee J. 117:398.

Bunch, Q. 1977*b*. More about purple loosestrife. Am. Bee J. 117:553.

Bunting, W. H. 1971. Portrait of a port: Boston, 1852–1914. The Belknap Press of Harvard University Press, Cambridge, Mass. xviii + 519 pp.

Bury, R. B. 1979. Review of the ecology and conservation of the bog turtle, *Clemmys muhlenbergii*. U.S. Fish Wildl. Serv., Spec. Sci. Rep.—Wildl. 219. 9 pp.

Christy, S. L., E. P. Karlander, and J. V. Parochetti. 1981. Effects of glyphosate on the growth rate of *Chlorella*. Weed Sci. 29:5–7.

Clapham, A. R., T. G. Tutin, and E. F. Warburg. 1962. Flora of the British Isles. 2nd ed. Cambridge University Press, Cambridge. xlviii + 1269 pp.

Coddington, J., and K. G. Field. 1978. Rare and endangered vascular plant species in Massachusetts. Committee for Rare and Endangered Species of the New England Botanical Club, Cambridge, Mass. 62 pp.

Cole, A. H. 1926. The American wool manufacture. Vol. 1. Harvard University Press, Cambridge, Mass. xii + 392 pp.

Correll, D. S., and H. B. Correll. 1975. Aquatic and wetland plants of southwestern United States. Vol. 2. Pages 857–1777. Stanford University Press, Stanford, Calif.

Cowardin, L. M., V. Carter, F. C. Golet, and E. T. LaRoe. 1979. Classification of wetlands and deepwater habitats of the United States. U.S. Fish Wildl. Serv., FWS/OBS-79/31. v + 103 pp.

Croizat, L. 1945. "Euphorbia Esula" in North America. Am. Midl. Nat. 33:231–243.

Dana, H. D. 1911. Two years before the mast. Houghton Mifflin Co., Boston. xiii + 553 pp.

Darwin, C. 1893. The different forms of flowers on plants of the same species. D. Appleton and Company, New York. viii + 352 pp.

Day, G. M. 1953. The Indian as an ecological factor in the northeastern forest. Ecology 34:329–346.

DeBach, P., editor. 1964. Biological control of insect pests and weeds. Reinhold Publishing Corp., New York. xxiv + 844 pp.

Deems, E. F., Jr., and D. Pursley, editors. 1978. North American furbearers. International Association of Fish and Wildlife Agencies in cooperation with the Maryland Department of Natural Resources—Wildlife Administration, Annapolis. x + 171 pp.

DeLoach, C. J. 1978. Considerations in introducing foreign biotic agents to control native weeds of rangelands. Proc. Int. Symp. Biol. Control Weeds, University of Florida, Gainesville. 4:39–50.

Dudley, W. R. 1886. The Cayuga flora. Part I. Bull. Cornell Univ. (Science) 2. xxx + 132 pp.

Dwight, T. 1823. Travels in New England and New York. Vol. 4. Wm. Baynes and Son, London. xi + 514 pp.

East, E. M. 1927. The inheritance of heterostyly in *Lythrum salicaria*. Genetics 12:393–414.

East, E. M. 1932. Further observations on *Lythrum salicaria*. Genetics 17:325–334.

Elton, C. S. 1958. The ecology of invasions. Methuen and Co. Ltd., London. 181 pp.

Emerson, F. B., Jr. 1961. Experimental establishment of food and cover plants in marshes created for wildlife in New York State. N.Y. Fish Game J. 8:130–144.

Faanes, C. A. 1979. Status of the black tern in western Wisconsin. Passenger Pigeon 41:124–128.

Fernald, M. L. 1940. The problem of conserving rare native plants. Smithson. Inst. Annu. Rep. (1939):375–391.

Fernald, M. L. 1950. Gray's manual of botany. 8th ed. American Book Company, New York. lxiv + 1632 pp.

Fogg, J. M., Jr. 1956. Weeds of lawn and garden. University of Pennsylvania Press, Philadelphia. xi + 215 pp.

Folmar, L. C., H. O. Sanders, and A. M. Julin. 1979. Toxicity of the herbicide glyphosate and several of its formulations to fish and aquatic invertebrates. Arch. Environ. Contam. Toxicol. 8:269–278.

Forbes, S. A. 1880. On some interactions of organisms. Ill. Nat. Hist. Surv. Bull. 1:1–17.

Forcella, F., and S. J. Harvey. 1983. Relative abundance in an alien weed flora. Oecologia (Berl.) 59:292–295.

Fredrickson, L. H., and T. S. Taylor. 1982. Management of seasonally flooded impoundments for wildlife. U.S. Fish Wildl. Serv., Resour. Publ. 148. 29 pp.

Friesen, G. 1966. Aquatic weed control studies in Manitoba. North Cent. Weed Control Conf. 21:42–43.

Gagnon, L. P. 1953. The control of purple loosestrife in La Commune at Baie du Febvre—1952. Proc. East. Sect. Natl. Weed Comm. Can. 6:135–136.

Gilbert, N., and S. B. Lee. 1980. Two perils of plant population dynamics. Oecologia (Berl.) 46:283–284.

Gleason, H. A. 1963. Illustrated flora of the northeastern United States and adjacent Canada. Vol. 2. New York Botanical Garden, Hafner Publishing Company, Inc., New York. iv + 655 pp.

Goeden, R. D. 1978. Part II: Biological control of weeds. Pages 357–414 *in* C. P. Clausen, ed. Introduced parasites and predators of arthropod pests and weeds: a world review. U.S. Dept. Agric. Handb. 480.

Gottrup, O., P. A. O'Sullivan, R. J. Schraa, and W. H. Vanden Born. 1976. Uptake, translocation, metabolism and selectivity of glyphosate in Canada thistle and leafy spurge. Weed Res. 16:197–201.

Goyer, R. A., and J. D. Stark. 1981. Suppressing water hyacinth with an imported weevil. La. Agric. 24:4–5.

Gray, A. 1869. Field, forest and garden botany. Ivison, New York. 386 pp.

Greeson, P. E., J. R. Clark, and J. E. Clark, editors. 1979. Wetland functions and values: the state of our understanding. American Water Resources Association, Minneapolis, Minn. x + 674 pp.

Grieve, M. 1923. Bee-plants and their honey.—VII. Bee World 4:196.

Grieve, M. 1959. A modern herbal. Vol. 2. Pages 431–888. Hafner Publishing Co., New York.

Grigson, G. 1955. The Englishman's flora. Phoenix House Ltd., London. 478 pp.

Haldane, J. B. S. 1936. Some natural populations of *Lythrum salicaria*. J. Genet. 32:393–397.

Halkka, O., and L. Halkka. 1974. Polymorphic balance in small island populations of *Lythrum salicaria*. Ann. Bot. Fennici 11:267–270.

Handlin, O. 1959. Immigration as a factor in American history. Prentice-Hall, Inc., Englewood Cliffs, N.J. ix + 206 pp.

Hara, H. 1956. Contributions to the study of variations in the Japanese plants closely related to those of Europe or North America. Part 2. J. Fac. Sci. Univ. Tokyo, Sect. III Bot. 6:343–391.

Haramis, G. M., and D. Q. Thompson. 1984. Survival of juvenile wood ducks in a northern greentree impoundment. J. Wildl. Manage. 48:1364–1369.

Haramis, G. M., and D. Q. Thompson. 1985. Density-production characteristics of box-nesting wood ducks in a northern greentree impoundment. J. Wildl. Manage. 49:429–436.

Harlow, A. F. 1926. Old towpaths. D. Appleton and Company, New York. xiv + 403 pp.

Harris, P. 1979. Cost of biological control of weeds by insects in Canada. Weed Sci. 27:242–250.

Hayes, B. 1979. Purple loosestrife—the wetlands honey plant. Am. Bee J. 119:382–383.

Heuch, I. 1980. Loss of incompatibility types in finite populations of the heterostylous plant *Lythrum salicaria*. Hereditas 92:53–57.

Holm, L., J. V. Pancho, J. P. Herberger, and D. L. Plucknett. 1979. A geographical atlas of world weeds. John Wiley & Sons, Inc., New York. xlix + 391 pp.

Howarth, F. G. 1983. Classical biocontrol: panacea or Pandora's box. Proc. Hawaii. Entomol. Soc. 24:239–244.

Howell, J. T., and G. H. True, Jr. 1966. Interesting plants from Nevada County, California. Leafl. West. Bot. 10:274–278.

Huffaker, C. B. 1959. Biological control of weeds with insects. Annu. Rev. Entomol. 4:251–276.

Hughes, R. 1977. Purple loosestrife judged a weed. Am. Bee J. 117:398.

Hultén, E. 1958. The amphi-Atlantic plants. Almqvist & Wiksell, Stockholm. 340 pp.

Hultén, E. 1964. The circumpolar plants. 1. Almqvist & Wiksell, Stockholm. (5) + 375 pp.

Hultén, E. 1971. The circumpolar plants. 2. Almqvist & Wiksell, Stockholm. 463 pp.

Hultén, E. 1972. Outline of the history of arctic and boreal biota during the Quaternary Period. Reprint of 1937 ed. J. Cramer Verlag, Stechert-Hafner Service Agency, Inc., New York. 168 pp.

Jaworski, E., and C. N. Raphael. 1979. Historical changes in natural diversity of fresh water wetlands, glaciated region of northern United States. Pages 545–557 *in* P. E. Greeson et al., eds. Wetland functions and values: the state of our understanding. American Water Resources Association, Minneapolis, Minn.

Jones, M. A. 1976. Destination America. Holt, Rinehart & Winston, New York. 256 pp.

Julien, M. H., editor. 1982. Biological control of weeds: a world catalogue of agents and their targets. Commonwealth Agricultural Bureau, Farnham Royal, Slough, England. 108 pp.

Kerner, A. 1902. The natural history of plants. (from the German by F. W. Oliver). Vol. 2. Blackie and Son, Limited, London. xi + 983 pp.

Kiviat, E. 1978. Bog turtle habitat ecology. Bull. Chic. Herpetol. Soc. 13:29–42.

Klingman, D. L., and J. R. Coulson. 1982. Guidelines for introducing foreign organisms into the United States for biological control of weeds. Weed Sci. 30:661–667.

Knowlton, C. H., and W. Deane. 1921. Reports on the flora of the Boston District—xxxiv. Rhodora 23:113–118.

Kraemer, H. 1916. Applied and economic botany. 2nd ed. Henry Kraemer, Philadelphia. viii + 822 pp.

Krapu, G. L., D. E. Facey, E. K. Fritzell, and D. H. Johnson. 1984. Habitat use by migrant sandhill cranes in Nebraska. J. Wildl. Manage. 48:407–417.

Leavitt, H. 1970. Superhighway—superhoax. Doubleday & Company, Inc., Garden City, N.Y. 324 pp.

Le Scal, Y. 1967. The great days of the Cape Horners. (L. Ortzen, transl.). The New American Library, New York. 175 pp.

Levin, D. A. 1970. Assortative pollination in *Lythrum*. Am. J. Bot. 57:1–5.

Levin, D. A., and H. W. Kerster. 1973. Assortative pollination for stature in *Lythrum salicaria*. Evolution 27:144–152.

Lichvar, R. W., and R. D. Dorn. 1980. Noteworthy collections. Madroño 27:138–141.

Linder, R. L., and D. E. Hubbard. 1982. Wetland values in the prairie pothole region of North America. Pages 27–39 *in* Proc. Great Plains Agric. Counc., North Platte, Nebr.

Lindroth, C. H. 1957. The faunal connections between Europe and North America. John Wiley & Sons, Inc., New York. 344 pp.

Linehan, D. 1982. Bugging the weeds: a look at integrated pest management. U.S. Fish Wildl. Serv. News, April/May:8–9.

Louis-Marie, Père. 1944. La Salicaire dans le Québec. Institut Agricole d'Oka. Province de Québec, Ministère de l'Agriculture. 46 pp.

Mace, H. 1976. The complete handbook of bee-keeping. Van Nostrand Reinhold Co., New York. 190 pp.

Mack, R. N. 1981. Invasion of *Bromus tectorum* L. into western North America: an ecological chronicle. Agro-Ecosystems 7:145–165.

Maddox, D. M., L. A. Andres, R. D. Hennessey, R. D. Blackburn, and N. R. Spencer. 1971. Insects to control alligatorweed. BioScience 21:985–991.

Malecki, R. A., and T. J. Rawinski. 1985. New methods for controlling purple loosestrife. N.Y. Fish Game J. 32:9–19.

Martindale, I. C. 1876. The introduction of foreign plants. Bot. Gaz. 2:55–58.

McKeon, W. H. 1959. A preliminary report on the use of chemical herbicides to control purple loosestrife (*Lythrum salicaria*) on a small marsh. Proc. Northeast. Weed Control Conf. 13:329–332.

McNaughton, S. J. 1968. Autotoxic feedback in relation to germination and seedling growth in *Typha latifolia*. Ecology 49:367–369.

Mead, R. M. 1957. The hunt for new honey plants. Am. Bee J. 97:300–301.

Meyer, B. H. 1969. History of transportation in the United States before 1860. Reprint of 1948 ed. Carnegie Inst. Publ. 215c. Washington, D.C. xi + 678 pp.

Mitchell, E. 1926. Germination of seeds of plants native to Dutchess County, New York. Bot. Gaz. 81:108–112.

Morse, R., and R. Palmer. 1925. British weeds. Ernest Benn, Limited, London. 207 pp.

Muenscher, W. C. 1955. Weeds. 2nd ed. The Macmillan Company, New York. xvi + 560 pp.

Nilsson, S. G., and I. N. Nilsson. 1978. Species richness and dispersal of vascular plants to islands in Lake Möckeln, southern Sweden. Ecology 59:473–480.

Ohio Writers' Project. 1940. The National Road. Ohio Historical Society, Columbus. 48 pp.

Ohwi, J. 1965. Flora of Japan. F. G. Meyer and E. H. Walker, eds. Smithsonian Institution, Washington, D.C. ix + 1067 pp.

Palhinha, R. T. 1939. Flora de Portugal. 2nd ed. Bertrand (Irmaos), Ltd., Lisbon. 938 pp.

Pammel, L. H. 1911. A manual of poisonous plants. The Torch Press, Cedar Rapids, Iowa. viii + 977 pp.

Pearsall, W. H. 1918. The aquatic and marsh vegetation of Esthwaite Water. J. Ecol. 6:53–74.

Pellett, F. C. 1947. American honey plants. 4th ed. Orange Judd Publishing Company, Inc., New York. 467 pp.

Pellett, M. 1944. Purple loosestrife spreads down river. Am. Bee J. 117:214–215.

Pellett, M. 1956. From the honey plant gardens. Am. Bee J. 96:198–199.

Perring, F. H., and S. M. Walters. 1976. Atlas of the British flora. Botanical Society of the British Isles, Wakefield, England. xxvi + 432 pp.

Polunin, O. 1969. Field guide: flowers of Europe. Oxford University Press, London. 662 pp.

Powell, J. W. 1962. Report on the arid regions of the United States. The Belknap Press of Harvard University Press, Cambridge, Mass. xxvii + 202 pp.

Radford, A. E., H. E. Ahles, and C. R. Bell. 1964. Guide to the vascular flora of the Carolinas. The Book Exchange, University of North Carolina, Chapel Hill. (i) + 383 pp.

Rawinski, T. J. 1982. The ecology and management of purple loosestrife (*Lythrum salicaria* L.) in central New York. M.S. thesis, Cornell University, Ithaca, N.Y. ix + 88 pp.

Rawinski, T. J., and R. A. Malecki. 1984. Ecological relationships among purple loosestrife, cattail and wildlife at the Montezuma National Wildlife Refuge. N.Y. Fish Game J. 31:81–87.

Ridley, H. N. 1930. The dispersal of plants throughout the world. L. Reeve & Co., Ltd., Ashford, Kent, England. xx + 744 pp.

Robbins, W. W., A. S. Crafts, and R. N. Raynor. 1942. Weed control. McGraw-Hill, New York. xi + 543 pp.

Room, P. M., K. L. S. Harley, I. W. Forno, and D. P. A. Sands. 1981. Successful biological control of the floating weed salvinia. Nature 294:78–80.

Rousseau, C. 1968. Histoire, habitat et distribution de 220 plantes introduites au Québec. Nat. Can. (Que.) 95:49–169.

Rueppel, M. L., B. B. Brightwell, J. Schaefer, and J. T. Marvel. 1977. Metabolism and degradation of glyphosate in soil and water. J. Agric. Food Chem. 25:517–528.

Salisbury, E. 1961. Weeds and aliens. Collins, London. 384 pp.

Schoch-Bodmer, H. 1936. The proportion of long-, mid- and short-styled plants in natural populations of *Lythrum salicaria* L. J. Genet. 36:39–43.

Schreiber, M. M. 1982. Modeling the biology of weeds for integrated weed management. Weed Sci. 30(suppl.):13–16.

Sernander, R. 1901. Den skandinaviska vegetationens spridningsbiologi (German summary). Lundequistska Bokhandeln, Upsala, Sweden. iv + 459 pp.

Shamsi, S. R. A., and F. H. Whitehead. 1974*a*. Comparative eco-physiology of *Epilobium hirsutum* L. and *Lythrum salicaria* L. 1. General biology, distribution and germination. J. Ecol. 62:279–290.

Shamsi, S. R. A., and F. H. Whitehead. 1974*b*. Comparative eco-physiology of *Epilobium hirsutum* L. and *Lythrum salicaria* L. 2. Growth and development in relation to light. J. Ecol. 62:631–645.

Shamsi, S. R. A., and F. H. Whitehead. 1977*a*. Comparative eco-physiology of *Epilobium hirsutum* L. and *Lythrum salicaria* L. 3. Mineral nutrition. J. Ecol. 65:55–70.

Shamsi, S. R. A., and F. H. Whitehead. 1977*b*. Comparative eco-physiology of *Epilobium hirsutum* L. and *Lythrum salicaria* L. 4. Effects of temperature and inter-specific competition and concluding discussion. J. Ecol. 65:71–84.

Shaw, S. P., and C. G. Fredine. 1956. Wetlands of the United States. U.S. Fish Wildl. Serv., Circ. 39. iv + 67 pp.

Shinners, L. H. 1953. Synopsis of the United States species of *Lythrum* (Lythraceae). Field Lab. 21:80–89.

Simberloff, D. 1985. Predicting ecological effects of novel entities: evidence from higher organisms. Pages 152–161 *in* Engineered organisms in the environment. Proc. Cross-discipl. Symp., Philadelphia, Pa. American Society for Microbiology, Washington, D.C.

Smith, A. H. 1867. On colonies of plants observed near Philadelphia. Proc. Acad. Nat. Sci. Phila. 19:15–24.

Smith, L. S. 1959. Some experiences with control of purple loosestrife at the Montezuma National Wildlife Refuge. Proc. Northeast. Weed Control Conf. 13:333–336.

Smith, R. H. 1964. Experimental control of purple loosestrife (*Lythrum salicaria*). N.Y. Fish Game J. 11:35–46.

Southwood, T. R. E. 1977. The relevance of population dynamic theory to pest status. Brit. Ecol. Soc. Symp. 18:35–54.

Spencer, N. R., and J. R. Coulson. 1976. The biological control of alligatorweed, *Alternanthera philoxeroides*, in the United States of America. Aquat. Bot. 2:177–190.

Stevens, R. W. 1871. On the stowage of ships and their cargoes. 5th ed. Longmans, Green, Reader, and Dyer, London. 817 pp.

Stevens, W. C. 1961. Kansas wild flowers. University of Kansas Press, Lawrence. 461 pp.

Stoudt, J. H. 1982. Habitat use and productivity of canvasbacks in southwestern Manitoba, 1961–72. U.S. Fish Wildl. Serv., Spec. Sci. Rep.—Wildl. 248. iv + 31 pp.

Stuckey, R. L. 1970. Distributional history of Epilobium hirsutum (great hairy willow-herb) in North America. Rhodora 72:164–181.

Stuckey, R. L. 1980. Distributional history of *Lythrum salicaria* (purple loosestrife) in North America. Bartonia 47:3–20.

Sutton, R. F. 1978. Glyphosate herbicide: an assessment of forestry potential. For. Chron. 54:24–28.

Sweet. R. 1839. The hothouse and greenhouse manual. Ridgway, London. 762 pp.

Tanner, H. S. 1970. Canals and railroads of the United States. Reprint of 1840 ed. A. M. Kelley, Publishers, New York. 272 pp.

Taylor, T. H. C. 1955. Biological control of insect pests. Ann. Appl. Biol. 42:190–196.

Thompson, D., and B. Yates. 1985. The purple peril. Wyo. Wildl. 49:14–15.

Thompson, D. Q., P. B. Reed, Jr., G. E. Cummings, and E. Kivisalu. 1968. Muck hardwoods as green-timber impoundments for waterfowl. Trans. North Am. Wildl. Nat. Resour. Conf. 33:142–159.

Thompson, D. Q., and R. H. Smith. 1970. The forest primeval in the Northeast—a great myth? Pages 255–265 *in* R. Komarek, ed. Proc. Tall Timbers Fire Ecol. Conf.

Thompson, W. R. 1930. The principles of biological control. Ann. Appl. Biol. 17:306–338.

Torrey, J., and A. Gray. 1840. A flora of North America. Vol. 1. Wiley and Putnam, New York. xiv + 711 pp.

Torrey, R. H. 1931. Field trips of the Club. Torreya 31:16–18.

Trauger, D. L. 1974. Looking out for the canvasback. Ducks Unltd. 38:12–15.

Tutin, T. G., V. H. Heywood, N. A. Burges, D. M. Moore, D. H. Valentine, S. M. Walters, and D. A. Webb, editors. 1968. Flora Europaea. Vol. 2. Cambridge University Press, Cambridge. xxvii + 455 pp.

U.S. Bureau of the Census. 1973. 1969 Census of agriculture. Vol. 5. Special reports. Part 10. Horticultural specialties. Table 6, p. 47. Washington, D.C.

U.S. Bureau of the Census. 1977*a*. 1974 Census of agriculture. Vol. 1. State and county data. Table 4, p. III–5. Washington, D.C.

U.S. Bureau of the Census. 1977*b*. 1974 Census of agriculture. Vol. 2. Statistics by subject. Part 6. Table 76, p. 88. Washington, D.C.

U.S. Fish and Wildlife Service. 1979. Another view—purple loosestrife alert. Am. Bee J. 119:383.

U.S. Fish and Wildlife Service. 1981. The Platte River ecology study. North. Prairie Wildl. Res. Cent., Spec. Res. Rep., Jamestown, N.Dak. xvi + 187 pp.

U.S. Fish and Wildlife Service and U.S. Bureau of the Census. 1982. 1980 national survey of fishing, hunting, and wildlife-associated recreation. U.S. Government Printing Office, Washington, D.C. viii + 156 pp.

U.S. Inland Waterways Commission. 1972. Preliminary report of the Inland Waterways Commission. Senate Doc. 325, 60th Congress, 1st session. Reprint of 1908 ed. Arno Press Inc., New York. vii + 701 pp.

U.S. Water and Power Resources Service. 1979. Water and land resource accomplishments, 1978. U.S. Government Printing Office, Washington, D.C. vii + 302 pp.

Van't Haaff, G. 1968. My experience with purple loosestrife. Am. Bee J. 108:244.

Wade, D. E. 1983. Commerce in alien, weedy plants under study, information sought. Restor. Manage. Notes 1:36.

Wade, D. E. 1985. Ethics and the prairie movement. Nat. Study 38:35,34.

Welker, W. V., and D. N. Riemer. 1982. Fragrant waterlily (*Nymphaea odorata*) control with multiple applications of glyphosate. Weed Sci. 30:145–146.

Wiegand, K. M., and A. J. Eames. 1926. The flora of the Cayuga Lake Basin, New York. Cornell Univ. Agric. Exp. Stn. Memoir 92. Ithaca, N.Y. 491 pp.

Wilson, F. 1964. The biological control of weeds. Annu. Rev. Entomol. 9:225–244.

Wilson, F. 1974. The use of biological methods in pest control. Pages 59–72 *in* D. Price Jones and M. E. Solomon, eds. Biology in pest and disease control. Blackwell Scientific Publications, Oxford, England.

Woodford, E. K., and S. A. Evans, editors. 1965. Weed control handbook. 4th ed. Blackwell Scientific Publications, Oxford, England. xv + 434 pp.

Wright, A. D., and T. D. Center. 1984. Biological control: its place in the management of water hyacinth. Pages 793–802 *in* G. Thyagarajan, ed. Proceedings of the International Conference on Water Hyacinth, Hyderabad, India, 7–11 February 1983. United Nations Environment Program, Nairobi, Kenya.

Wright, C. W. 1910. Wool-growing and the tariff. Houghton Mifflin Co., Boston. xiii + 362 pp.

Zimmerman, E. C. 1958. Insects of Hawaii. Vol. 7, Macrolepidoptera. University of Hawaii Press, Honolulu. ix + (i) + 542 pp.

Zohary, M. 1972. Flora Palaestina. Part 2. The Israel Academy of Sciences and Humanities, Jerusalem. 489 pp.

Thompson, Daniel Q., Ronald L. Stuckey, and Edith B. Thompson. 1987. **Spread, impact, and control of purple loosestrife (*Lythrum salicaria*) in North American wetlands.** U.S. Fish Wildl. Serv., Fish Wildl. Res. 2. 55 pp.

Purple loosestrife (*Lythrum salicaria*) is an erect, perennial herb of Eurasian origin that has spread across the wetlands of mid-latitude North America. It has permanently displaced native emergent vegetation and is a threat to riparian pastures and hay meadows. The origin, uses, history of spread, and ecology of this weed are reviewed. Its impacts on North American habitats and native biota are described; recommendations for containment and control are made.

Key words: Purple loosestrife, *Lythrum salicaria*, origin, distribution, ecology, spread, impact, uses, control.

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The following is a list of recent *Fish and Wildlife Research* publications.

1. Life History and Status of the Endangered Cui-ui of Pyramid Lake, Nevada, by G. Gary Scoppettone, Mark Coleman, and Gary A. Wedemeyer. 1986. 23 pp.

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